MORPHOLOGY AND PHENETICS OF RHIZOPHORACEAE POLLEN[1]

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ABSTRACT

Pollen morphologic data from light, scanning, and transmission electron microscopy were used in a phenetic analysis to assess variation within and among the four tribes traditionally included in Rhizophoraceae: Anisophylleeae, Gynotrocheae, Macarisieae, and Rhizophoreae. Principal components analysis revealed that pollen of Anisophylleeae is phenetically divergent from that of Gynotrocheae, Macarisieae, and Rhizophoreae, and therefore we recognize this taxon at the family level, Anisophylleaceae. In contrast Rhizophoraceae sensu stricto forms a phenetic continuum, with pollen of Macarisieae intermediate between Gynotrocheae and Rhizophoreae. Endoapertures of Anisophylleaceae pollen, when present, are circular and poorly defined, whereas all species of Rhizophoraceae possess endoapertures with some degree of fusion. Pollen of both families has a generalized angiosperm morphology, thereby providing no palynological basis for assessing relationships to Myrtales or other groups.

Comparative palynology in Rhizophoraceae has focused on the mangrove genus *Rhizophora*, primarily in connection with the recognition and study of paleo-shorelines (Kuprianova, 1959; Langenheim et al., 1967; Assemien, 1969; Rakosi, 1978; Sowunmi, 1981). Consequently, several species of *Rhizophora* have been well documented. Langenheim et al. (1967) used light microscope data (pollen shape and a unique endoaperture system) to characterize *R. mangle*, *R. samoensis*, *R. racemosa*, and *R. harrisonii*. Muller & Caratini (1977) expanded the study of modern Rhizophoraceae by employing transmission electron microscopy (TEM) in addition to light microscopy (LM) and scanning electron microscopy (SEM). Their analysis included three species studied by Langenheim et al. (1967), *R. mangle*, *R. racemosa*, and *R. harrisonii*, as well as *R. mucronata*, *R. stylosa*, *R. apiculata*, *R. lamarckii*, and *R. brevistyla*. Muller & Caratini (1977) essentially confirmed the findings of Langenheim et al. (1967), but underscored that most LM characters exhibit too much overlap to separate species. Although their study lacked the benefit of comparison with other Rhizophoreae (*Bruguiera*, *Ceriops*, and *Kandelia*), as well as other members of the family, they subdivided the *Rhizophora* pollen type into four groups by combining LM data with an SEM analysis of sculpture patterns.

Typically, other pollen studies of the family were accomplished as part of floristic or general morphologic surveys (Erdtman, 1952; Kubitzki, 1965; Huang, 1968; Guers, 1974; Geh & Keng, 1974; Sowunmi, 1974; Straka & Friedrich, 1984; Thanikaimoni, 1986a, 1987). SEM studies have been centered on the tribe Rhizophoreae (Tissot, 1979; Bertrand, 1983; Ludlow-Wiechers & Alvarado, 1983). For complete references to pollen studies in the family, see Thanikaimoni (1972, 1973, 1976, 1980, 1986b).

Little palynologic attention has been directed specifically to the taxonomic integrity within and among the four tribes traditionally included in Rhizophoraceae sensu lato: Anisophylleeae, Gynotrocheae, Macarisieae, and Rhizophoreae. Using LM, SEM, and TEM, we investigated the pollen morphology of all genera in these taxa. Of particular interest is Anisophylleeae, which on the basis of a broad array of characters has been considered to constitute a distinct family, Anisophylleaceae (see other symposium papers). With this in mind, we

[1] *This study was partially supported by grants from the National Science Foundation to J.J.S. (BSR-83155186) and P.H.R. We gratefully acknowledge the help of Daniel J. Hough and Henry Loconte, University of Oklahoma, for many suggestions in developing the phenetic analysis, and of Gary D. Schnell and James R. Estes, University of Oklahoma, for reviewing the completed manuscript.*

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TABLE 1. *Taxa examined, collection data, and plate references.*

OTU	Taxa	Location	Collector/Herbarium	Figures SEM	Figures TEM
	Anisophyllea buttneri Engl.	Gabon	*Thollon 4130* (MO)	2	
A1	*A. disticha* (Jack.) Baill.	Singapore	*Kiah & Leong s.n.* in 1984 (no voucher)	4	36
A2	*A. fallax* Scott Elliot	Madagascar	*Reserves Nat. 2619* (TAN)		40
	A. laurina R. Br.	West Africa	*Fairchild s.n.* in 1927 (US)	1	41
A3	*A. obtusifolia* Engl. & Brehmer	Tanzania (Usambara Mountains)	*Amani River Institute s.n.* (no voucher), Bukit Timah Natural Reserve	3	38, 39
	Combretocarpus rotundatus (Miq.) Dans.	N Borneo	*Tandom 2816* (K)		37
A4	*C. rotundatus*	Brunei	*Juncosa s.n.* in 1983 (no voucher)	7, 8	
A5	*Poga oleosa* Pierre	Cameroon	*Thomas 2273* (MO)	5	
	P. oleosa	Nigeria	*Coombe 186* (K)		43
A6	*Polygonanthus amazonicus* Ducke	Brazil	*Zarucchi 3138* (US)	9	
	P. amazonicus	Brazil	*Pires 1281* (NY)		42
	P. amazonicus	Brazil	*S. R. Hill 12922* (MO)	6	
G1	*Carallia brachiata* (Lour.) Merr.	Australia	*Jackes s.n.* in 1983 (JCT)	35	44
G2	*C. eugenioides* King	Malaysia	*B. C. Stone 15114* (KLU)	33, 34	45
	Crossostylis biflora Forst. (*C. raiateensis* J. W. Moore)	Society Islands	*St. John 17346* (MO)		
G3	*C. grandiflora* (Pancher ex Brogn. & Gris.	New Caledonia	*McPherson 6331* (MO)	31	
	C. grandiflora	New Caledonia	*McPherson 1898* (MO)		46
G4	*Gynotroches axillaris* Blume	Malaysia	*B. C. Stone 15397* (KLU)	30	47
G5	*Pellacalyx* cf. *saccardianus* Scortech.	Malaysia	*B. C. Stone 15396* (KLU)	32	49
	P. pustulata Merr.	Philippines	*Wenzel 1497* (MO)		48
	Anopyxis ealeaensis Sprague	Belgian Congo	*Germain 191* (MO)	23	50
M1	*A. kleineana* (Pierre) Engl.	Cameroon	*Thomas 3464* (MO)	22	51
	Blepharistemma membranifolia (Miq.) Ding Hou	India	*Wallich 1832* (K)		59
M2	*B. membranifolia*	India	*Manilal s.n.* in 1984 (no voucher)	17	
	Cassipourea afzelii (Oliv.) Alston	Liberia	*Baldwin 10609* (MO)	18	
M3	*C. elliptica* (Sw.) Poir.	Panama	*Kirkbride & Duke 1322* (MO)		58
	C. guianensis Aubl.	Brazil	*Nelson 1324* (MO, NY)	19	
	C. gummiflora Tul. var. *verticillata* (N. E. Br.) J. Lewis	Zimbabwe (cultured Harare Bot. Gard.)	*Muller 3558* (SRGH)	21	
	Compiphyton gabonense Floret	Gabon	*Le Tetsu 5918* (P)	10	
M4	*C. gabonense*	Zaire	*Germain 5213* (BR)		62
M5	*Dactylopetalum sessiliflorum* Benth.	Madagascar	*Reserves Nat. 4327* (TAN)	20	60
	D. zenkeri Engl.	Cameroon	*Zenker 4701* (MO)		61
M6	*Macarisia ellipticifolia* Arènes	Madagascar	*Service For. 1972* (TAN)	14	55
	M. humbertiana Arènes	Madagascar	*Humbert 23505* (P)	15	56
	M. lanceolata Baill.	Madagascar	*Service For. 9366* (P)	13	54
	M. lanceolata	Madagascar	Serv. Eaux & Forêt 2955 (TAN)		

TABLE 1. *Continued.*

OTU	Taxa	Location	Collector/Herbarium	Figures SEM	Figures TEM
M7	*M. pyramidata* Thou.	Madagascar	*Service For. 9741* (P)	16	57
	Petalodactylus obovata Arènes	Madagascar	*Alaotra Agric. Sta. 3868* (TAN)		63
M8	*Sterigmapetalum heterodoxum* Steyerm.	Venezuela	*Wingfield 13245* (MO)	11	53
M9	*S. obovatum* Kuhlm.	Brazil	*Maguire et al. 56502* (MO)	12	52
	Bruguiera gymnorrhiza (L.) Lamk.	Madagascar	*Alaotra Agric. Sta. 27552* (TAN)		68
R1	*B. gymnorrhiza*	Madagascar	*Reserves Nat. 9255* (TAN)	28	
	Ceriops tagal (Perr.) C. B. Rob.	Madagascar	*Hervien s.n.* (TAN)		
R2	*C. tagal*	Madagascar	*Dorr & Koenders 3063* (MO)	27	69
R3	*Kandelia candel* (L.) Druce	Japan	*Murata & Nakamura 1142* (MO)	29	67
R4	*Rhizophora mangle* L.	Florida (cultivated)	*Tobe s.n.* in 1981 (no voucher; Fairchild Botanical Garden)	24	66
R5	*R. mucronata* Lamk.	Mozambique	*Torre & Paiva 11483* (MO)		
R6	*R. mucronata*	Madagascar	*Bosser 9947* (TAN)		64
	R. mucronata	Madagascar	*Hervien s.n.* in 1964 (TAN)		
	R. mucronata	Madagascar	*Marot 2602* (TAN)	25	
R7	*R. stylosa* Griff.	Florida (cultivated)	*Tobe s.n.* in 1981 (no voucher; Fairchild Botanical Garden FG69-111)	26	65

conducted a phenetic analysis to assess overall morphologic variation within and among these groups and to test the hypothesis of separate familial status for Anisophylleaceae.

MATERIALS AND METHODS

POLLEN MORPHOLOGY

In our investigation, pollen from 51 collections (representing 39 species of Anisophylleaceae and Rhizophoraceae) was examined by light and electron microscopy (Table 1). Hereinafter, Rhizophoraceae is referred to in the strict sense (i.e., only the tribes Gynotrocheae, Macarisieae, and Rhizophoreae). All pollen were initially treated with the acetic anhydride/sulfuric acid acetolysis mixture of Erdtman (1960). For LM, whole grains were mounted in glycerine jelly and observed with a Leitz Ortholux microscope using transmitted light. Measurements (μm) were based on 10–50 undistorted grains when possible. Pollen for SEM was either air dried from 95% ethanol or critical-point dried, sputter coated with gold, and examined with either an ISI Super II SEM or ETEC Autoscan SEM. Pollen for TEM was processed as reported earlier (Skvarla, 1966) and examined with either a Philips model 200 TEM or Zeiss 10 TEM.

PHENETIC ANALYSIS

Operational Taxonomic Units (OTUs). Data from 27 collections (Table 1) were subjected to a numerical phenetic analysis as Operational Taxonomic Units (OTUs; Sneath & Sokal, 1973). These 27 OTUs represent 26 species (*Rhizophora mucronata* has two OTUs) and were selected if data were obtained for all 33 characters (Table 2).

Characters. The 33 characters (Table 2) used in the phenetic analysis are based on standard palynological data (Erdtman, 1952; Faegri & Iversen, 1975), and include 10 LM (1–10), 13 SEM (11–23), and 10 TEM (24–33) characters. Although most are self-explanatory, several merit elaboration. The variability in polar axis (P) and breadth (E) is often expressed in terms of range or minimum and maximum measurements. We used standard deviation (characters 2 and 4) in-

TABLE 2. *Characters used in numerical analysis.*

Polar axis (P)
1. Mean
2. Standard deviation (SDP)

Greatest breadth (E)
3. Mean
4. Standard deviation (SDE)
5. Polar axis/greatest breadth (P/E)
6. Endoaperture fusion (EF)

Completely unfused	0
Mostly unfused (< 40%)	1
Mixed (approx. 50%)	2
Mostly fused (> 60%)	3

7. Mean polar length of endoaperture (PL)
8. Endoapertural index (EI)
9. Mean distance between colpal ends (DCE)
10. Polar area index (PAI)

Sculpture of mesolcolpia		Sculpture of poles	
11. Psilate	(PS)	15. Psilate	(PS)
12. Punctate	(PU)	16. Punctate	(PU)
13. Rugulate	(RU)	17. Rugulate	(RU)
14. Striate	(ST)	18. Striate	(ST)

Sculpture of mesocolpial margins
19. Psilate (PS)
20. Punctate (PU)
21. Rugulate (RU)
22. Spinulate (SP)
23. Striate (ST)

Exine structure

24. Tectum thickness	(TT)
25. Height of columellae	(CH)
26. Maximum width of columellae	(CW)
27. Foot layer thickness	(FL)
28. Endexine thickness	(EN)
29. Tectum thickness ratio	(TT/TET*)
30. Columellar height ratio	(CH/TET)
31. Foot layer thickness ratio	(FL/TET)
32. Endexine thickness ratio	(EN/TET)
33. Intercolumellar granulation	(IG)
No granulation	0
Incipient granulation (< 50%)	1
Abundant granulation (> 50%)	2

* TET = total exine thickness.

stead, because it is based on all grains measured and is less affected by sample size or aberrant grains. Character 6, endoaperture fusion, expresses information usually included for Rhizophoraceae pollen (e.g., Muller & Caratini, 1977). It is an ordered multistate character based on increasing percentage of endoaperture fusion and was processed in the same way as quantitative characters (Sneath & Sokal, 1973). Character 8, endoapertural index (EI), is the ratio of polar length of the endoaperture (PL) to polar axis (P). It is a ratio we have constructed to express the relative width of the endoaperture.

The 13 SEM characters describe the sculpture of three parts of the pollen surface: mesocolpia (11–14), poles (15–18), and mesocolpial margins (19–23). Although this information can be condensed into three unordered multistate characters, only ordered multistate characters are acceptable with principal components analysis (Gower, 1966). Therefore, as Gower (1966) recommended, we used binary (0, 1) characters to indicate absence (0) or presence (1) of a particular sculpture pattern.

TEM characters 24–28 were recorded as means of measurements (μm) taken from an average of six negatives. All measurements were mid-mesocolpial on equatorial sections perpendicular to the polar axis. Character 33 is an ordered multistate character based on increasing percentage of intercolumellar granulation. The remaining characters (29–32) are expressions of exine shape, that is, the relative contribution of tectum, columellae, foot layer, and endexine to the total exine thickness. In five cases it was necessary to take TEM data from a different collection of the same species (Table 3). This procedure was followed to insure adequate representation of all taxa.

Numerical Analysis. Phenetic variation was analyzed using NT-SYS (Rohlf et al., 1982), a package of multivariate computer programs designed for use in systematics. The data (Table 3) were standardized (i.e., each character being transformed to have a mean of zero and standard deviation of one), followed by calculation of a Pearson product-moment correlation matrix and principal components analysis (Sneath & Sokal, 1973). A minimum spanning tree (Dunn & Everitt, 1982) was calculated using an average taxonomic distance matrix (Sneath & Sokal, 1973) produced from the standardized data set.

Principal components analysis also produces a matrix of eigenvectors showing character loadings on each component (Table 5). If a character has a loading of 0.9 on component I, then $(0.9)^2$ or 0.81 (81%) of that character is expressed or statistically "explained" on component I and the remaining 19% on other components. Table 5 lists all characters with loadings greater than 0.5. If a character has a positive (+) loading, then OTUs with higher values for that character tend to be found toward the positive end of that component. Higher values include larger quantitative mea-

surements, higher-numbered multistate character states, and binary (0, 1) characters with character state 1.

Results

Pollen Morphology

Detailed LM, SEM, and TEM measurements and observations for 27 collections (Table 1) are given in Table 3, and summarized for Anisophylleaceae and each tribe of Rhizophoraceae in Table 4. The supplemental descriptions below include characters not considered in the numerical analysis, as well as unique morphological features in need of emphasis. Morphological delineation is based on all 51 collections (Table 1).

Anisophylleaceae

LM. Pollen is mainly tricolporoidate (occasionally tricolporate), rarely with two apertures, radially symmetrical, and isopolar. Syncolpate grains are common. Endoapertures, when present, are circular but poorly defined.

SEM (Figs. 1–9). Of special note is *Anisophyllea disticha*, which differs markedly from all other species in this study by having a striate surface.

TEM (Figs. 36–43). In *A. disticha* and *A. obtusifolia*, a narrow and highly undulating columellae layer is present in sectional planes near the equator (Figs. 36, 38). In a different sectional plane of *A. obtusifolia*, and in *A. laurina*, the columellae layer is straight, and the foot layer is thinner than the tectum (Figs. 39, 41).

Gynotrocheae

LM. Pollen is tricolporate, radially symmetrical, and isopolar. Endoapertures in all grains are fused laterally, the only tribe so distinguished.

SEM (Figs. 30–35). A psilate–punctate surface is dominant in this tribe.

TEM (Figs. 44–49). In *Crossostylis grandiflora* a trace of granular matrix similar to that described for Macarisieae (see below) is present at the lower tectum margin (Fig. 46). *Pellacalyx* differs from other Gynotrocheae by having a thin tectum and tall, branched columellae that become shorter at the poles (Figs. 48, 49); granules are suggested beneath the lower tectum margin and the distal parts of the columellae.

Macarisieae

LM. Pollen is tricolporate, rarely dicolporate and tetracolporate, radially symmetrical, and isopolar. Shape has the greatest range of the tribes, from suboblate to prolate (character 5, Table 3).

SEM (Figs. 10–23). This tribe processes variable pollen sculpture (Table 4).

TEM (Figs. 50–63). Intercolumellar spaces are either partially or completely filled with a matrix of granules (Figs. 50, 52, 54, 55, 57, 59). Some columellae also are granular distally. In taxa with prominent fused (zonorate) endoapertures (character 6, Table 2), the endexine is granular in the mesocolpia in the vicinity of the endoaperture.

Rhizophoreae

LM. Pollen is tricolporate, radially symmetrical, and isopolar (except some grains in *Rhizophora mucronata*).

SEM (Figs. 24–29). Pollen of *R. mucronata* has a basically punctate–rugulate surface. However, this pattern varies among the five collections examined (Table 1), as well as within collections. In the collection *A. Torre & J. Pavia 11483* rugulate elements are distinct; some grains in this collection showed a punctate–rugulate surface on one hemisphere and a psilate–punctate surface on the other. Dicolporate grains were common. In the collection *J. Bossier 9947* the surface has a faint rugulate–punctate sculpture, while in the collection *Greve 290* it is psilate–punctate. In the collection *Hervien s.n.*, made in 1964, the pollen grains are psilate–punctate, faintly rugulate–punctate, or distinctly rugulate–punctate. Some dicolporate grains are also present in this collection. In the collection *P. Marot 2602* the grains are rugulate–punctate; some also have spinules. Note that spinules were present on the mesocolpial margins of *Carallia brachiata* (Fig. 35), *C. eugenioides* (Figs. 33, 34), and *Gynotroches axillaris* (Fig. 30).

TEM (Figs. 64–69). Tectum thickness is the most variable of the four groups (character 24, Table 3).

Phenetic Analysis

Principal components analysis reveals two phenetically distinct groups of OTUs (Fig. 70). One group, consisting of all Anisophylleaceae OTUs, is located toward the positive end of component I and the negative end of component II. The first two components account for 25.5 and 20.7% of the total variation. The other group is an elongated continuum formed by the three tribes of Rhizophoraceae, with Macarisieae OTUs distributed across phenetic space between Rhizophoreae and Gynotrocheae. The minimum spanning tree indicates

TABLE 3. *Data set used in numerical analysis.*[1]

OTU	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
A1	22	1.2	16	0.8	135	0	2	.08	3	.17	0	0	0	1	0	0
A2	28	3.5	17	3.0	164	0	0	.00	2	.09	0	1	0	0	0	1
A3	26	1.7	20	1.7	131	0	2	.09	3	.14	0	1	0	0	0	1
A4[2]	20	1.2	17	1.7	118	0	0	.00	3	.16	0	1	0	0	0	1
A5[2]	29	2.6	22	1.7	133	0	3	.10	4	.17	0	1	0	0	0	1
A6[2]	28	1.6	25	1.6	114	0	0	.00	5	.17	0	1	0	0	0	1
G1	14	0.6	12	0.6	117	3	2	.27	3	.22	1	1	0	0	1	1
G2	17	1.5	14	1.0	125	3	5	.27	3	.18	1	1	0	0	1	1
G3[2]	15	0.9	14	0.8	105	3	5	.30	2	.14	1	1	0	0	1	1
G4	15	3.0	12	2.3	122	3	4	.29	3	.23	1	1	0	0	1	1
G5	11	1.2	8	0.7	124	3	2	.23	1	.17	1	0	0	0	1	0
M1	24	1.3	22	1.8	106	3	4	.16	4	.15	1	0	0	0	1	0
M2[2]	19	1.6	18	1.1	107	3	4	.19	5	.27	0	1	1	0	0	1
M3	20	1.7	15	1.3	133	2	3	.13	4	.26	0	1	0	0	0	1
M4	17	0.6	13	1.4	129	1	2	.10	2	.11	0	1	0	0	1	0
M5	17	1.2	15	1.4	109	1	2	.10	3	.20	0	1	0	0	0	1
M6	12	0.9	13	0.9	88	3	1	.11	2	.17	1	0	0	0	1	0
M7	13	1.5	14	0.9	97	1	1	.07	3	.26	0	1	1	0	1	1
M8	19	2.5	20	1.7	85	3	5	.25	4	.19	1	0	0	0	1	0
M9	14	1.1	16	1.4	86	3	2	.16	3	.21	0	1	1	0	0	1
R1	18	1.0	19	1.1	93	2	2	.13	5	.27	0	1	1	0	0	1
R2	13	1.0	14	1.2	92	3	3	.19	4	.27	0	1	1	0	0	1
R3	20	1.2	22	1.5	92	1	3	.16	4	.21	0	1	1	0	0	1
R4	19	1.0	19	0.9	103	3	3	.17	5	.28	0	1	1	0	0	1
R5	23	1.3	21	1.4	107	3	3	.11	6	.32	0	1	1	0	0	1
R6	24	1.8	21	1.5	113	3	4	.18	5	.25	0	1	1	0	0	1
R7	23	1.2	23	1.4	100	1	4	.17	5	.22	0	1	1	0	0	1

[1] OTU symbols from Table 1 (column 1), characters as in Table 2.

[2] The TEM data for A4, A5, G3, and M2 were taken from the other collection of the same species (Table 1). The TEM data for A6 were taken from the *Pires 1281* collection.

considerable distortion within Gynotrocheae (Fig. 70). Relationships within this tribe are clarified by including component III, which accounts for an additional 13.0% of the total variation (Fig. 71). Component III also reveals marked divergence between *Anisophyllea disticha* (A1) and the other Anisophylleaceae OTUs.

OTUs are distributed across component I based on overall size, tectum thickness, collumellae height, and other characters (Table 5). Thus the larger grains of Anisophylleaceae and Rhizophoreae are to the right (Fig. 70), and the smaller Gynotrocheae pollen is to the left. Anisophylleaceae and Rhizophorea OTUs separate along component II because of differences in sculpture, shape, and other characteristics (Table 5).

TABLE 4. *Summary of data in Table 3 for Anisophylleaceae and each tribe of Rhizophoraceae.*[1]

OTU	Characters															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
AA	26	2.0	20	1.7	133	0	1	.05	3	.15	0	1	0	0	0	1
GG	14	1.4	12	1.1	119	3	4	.27	2	.19	1	1	0	0	1	1
MM	17	1.4	17	1.3	104	3	3	.14	3	.20	0	1	0	0	1	1
RR	20	1.2	20	1.3	100	3	3	.16	5	.26	0	1	1	0	0	1

[1] AA = Anisophylleaceae, GG = Gynotrocheae, MM = Macarisieae, RR = Rhizophoreae. All measurement characters have been averaged. For binary (SEM) characters, the predominant state is given and underlined to indicate one or more exceptions within the family or tribe. For multistate characters 6 and 33, the median is given.

TABLE 3. *Continued.*

Characters																
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0	1	0	0	0	0	1	.58	.18	.15	.38	.13	.46	.14	.30	.10	0
0	0	0	1	0	0	0	.47	.28	.23	.34	.14	.38	.23	.28	.11	0
0	0	0	1	0	0	0	.68	.28	.23	.43	.12	.45	.19	.28	.08	0
0	0	1	0	0	0	0	.37	.36	.19	.27	.07	.35	.34	.25	.07	0
0	0	0	1	0	0	0	.41	.46	.15	.09	.14	.37	.42	.08	.13	0
0	0	0	1	0	0	0	.71	.28	.26	.98	.18	.33	.13	.46	.08	0
0	0	0	0	0	1	0	.16	.08	.11	.20	.14	.28	.14	.34	.24	0
0	0	0	0	0	1	0	.25	.05	.11	.26	.23	.32	.06	.33	.29	0
0	0	1	1	0	0	0	.27	.05	.07	.14	.13	.46	.08	.24	.22	1
0	0	0	0	0	1	0	.28	.06	.14	.26	.22	.34	.07	.32	.27	0
0	0	1	0	0	0	0	.16	.07	.08	.12	.13	.33	.15	.25	.27	1
0	0	1	0	0	0	0	.36	.09	.19	.51	.08	.35	.09	.49	.08	2
0	0	0	1	1	0	0	.27	.09	.10	.30	.07	.37	.12	.41	.10	2
0	0	0	1	0	0	0	.20	.11	.12	.15	.08	.37	.20	.28	.15	0
0	0	1	0	0	0	0	.40	.07	.11	.43	.09	.40	.07	.43	.09	2
0	0	1	0	0	0	0	.30	.08	.14	.31	.10	.38	.10	.39	.13	1
0	0	1	0	0	0	0	.30	.10	.11	.30	.07	.39	.13	.39	.09	2
0	0	1	1	0	0	0	.17	.08	.08	.20	.05	.34	.16	.40	.10	2
0	0	1	0	0	0	0	.54	.19	.13	.77	.05	.35	.12	.50	.03	2
1	0	0	1	1	0	0	.31	.12	.11	.37	.01	.38	.15	.46	.01	2
1	0	0	1	1	0	0	.31	.11	.14	.35	.03	.39	.14	.44	.04	0
1	0	0	1	1	0	0	.17	.08	.11	.26	.09	.28	.13	.43	.15	0
1	0	0	1	1	0	0	.40	.12	.12	.59	.14	.32	.10	.47	.11	0
1	0	1	1	1	0	0	.36	.13	.19	.56	.05	.33	.12	.51	.05	0
1	0	0	1	1	0	0	.35	.21	.27	.57	.03	.30	.18	.49	.03	0
1	0	0	1	1	0	0	.51	.19	.22	.41	.06	.44	.16	.35	.05	0
1	0	1	0	0	0	0	.38	.14	.19	.46	.11	.35	.13	.42	.10	0

The minimum spanning tree interconnects Gynotrocheae OTUs with two short and two long links (Fig. 71). The short connections are *Carallia eugenioides* (G2) to *C. brachiata* (G1) and *Gynotroches axillaris* (G4) at distances of 0.630 and 0.636, respectively. *Pellacalyx* cf. *saccardianus* (G5) joins *C. brachiata* (G1) and *Crossostylis grandiflora* (G3) at distances of 1.035 and 1.023.

Connections within Macarisieae average 0.793, but only one OTU (*Dactylopetalum sessiliflorum*, M5) links with more than two other OTUs within the tribe. The congeneric OTUs *Sterigmapetalum heterodoxum* (M8) and *S. obovatum* (M9) are separated by a distance of 1.377. *Sterigmapetalum obovatum* (M9) is actually more similar (0.603) to *Bruguiera gymnorrhiza* (R1) than to any OTU of its own tribe.

Most Rhizophoreae are directly linked to *Bru-*

TABLE 4. *Continued.*

Characters																
17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33
0	0/0	0/0	1/0	0	0	0/0	.54	.31	.20	.42	.13	.39	.24	.28	.10	0
0	0	0/0	0/0	0	1/0	0	.22	.06	.10	.20	.17	.35	.10	.30	.26	0
0/0	0	1/0	0/0	0/0	0	0	.32	.10	.12	.37	.07	.38	.13	.42	.09	2
1/1	0	0/1	1/1	1/1	0	0	.35	.14	.18	.46	.07	.34	.14	.44	.08	0

TABLE 5. *Character loadings from principal components analysis.*[1]

Direction	Loadings	I	II	III
+	.80–.89		13	
	.70–.79	1, 3, 26	10, 17, 21	16
	.60–.69	9, 20, 24, 25	6, 31	12
	.50–.59		9	22, 28, 32
–	.80–.89	11, 15		
	.70–.79		5	
	.60–.69	8, 32		
	.50–.59	6	25, 28	14, 18, 23, 33

[1] Numbers under each component refer to characters outlined in Table 2. Only characters with loadings greater than 0.5 are shown.

guiera gymnorrhiza (R1), with two exceptions (R5 and R7) which are two links away. The links within Rhizophoreae are the shortest of any tribe, averaging 0.639. In a similar manner, all Anisophylleaceae OTUs are joined to *Anisophyllea obtusifolia* (A3) but at much longer distances (lower similarity) than those within Rhizophoreae. Even discounting *A. disticha* (A1), links within Anisophylleaceae average 0.923, higher than any tribe of Rhizophoraceae. A1 joins A3 from a distance of 1.796, the longest link on the minimum spanning tree. *Anisophyllea disticha* is actually more similar to three Macarisieae OTUs than to *Combretocarpus rotundatus* (A4), the next closest OTU within Anisophylleaceae. The closer Macarisieae OTUs are *Cassipourea elliptica* (M3), *Comiphyton gabonense* (M4), and *Dactylopetalum sessiliflorum* (M5).

Intertribal links are shorter than many intratribal connections. *Blepharistemma membranifolia* (M2), for example, is more similar to R1 (0.702) than to either M3 (0.833) or M9 (0.718). Likewise, *Macarisia ellipticifolia* (M6) is more similar to G5 (0.819) than to either M1 (0.906) or M4 (0.850).

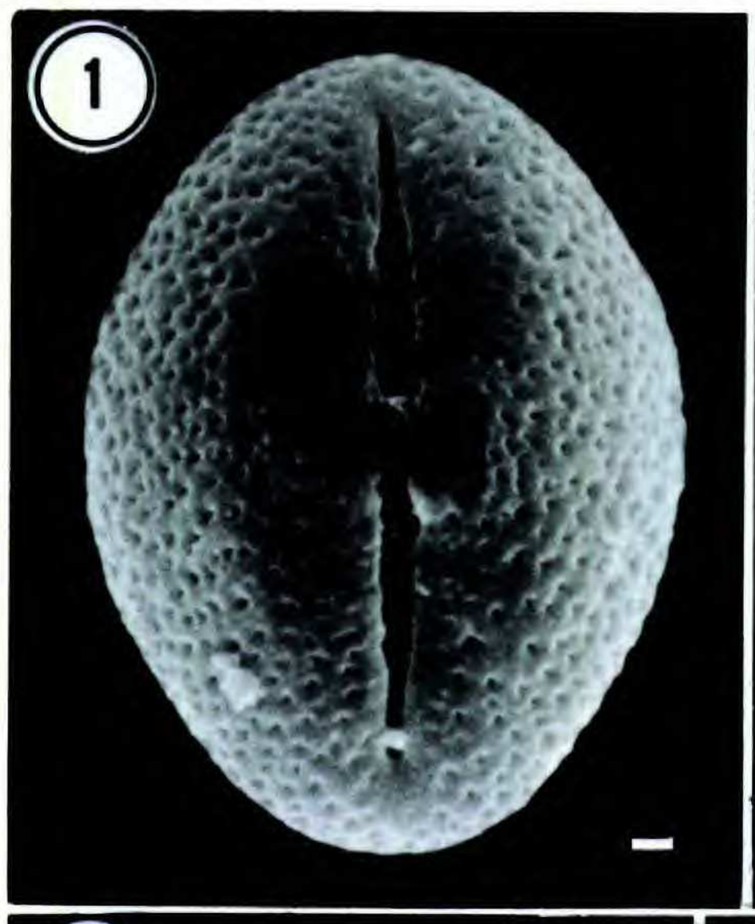
The phenetic gap between Anisophylleaceae and Rhizophoraceae is spanned by a link between *Combretocarpus rotundatus* (A4) and *Dactylopetalum sessiliflorum* (M5) at a distance of 0.913. Although this is greater than intertribal connections within Rhizophoraceae, it is shorter than several links within Anisophylleaceae.

→

FIGURES 1–12. *Scanning electron micrographs of Anisophylleaceae (1–9) and Macarisieae (10–12) pollen.—1.* Anisophyllea laurina, *lateral view, surface punctate.—2.* A. buttneri, *polar view.—3.* A. obtusifolia. *Portion of mesocolpium showing punctate surface.—4.* A. disticha, *lateral view. This species differs from the others in having a striate surface.—5.* Poga oleosa, *polar view.—6.* Polygonanthus amazonicus, *polar view.—7, 8.* Combretocarpus rotundatus.—*7. Polar view.—8. Sublateral view of a dicolporate, syncolpate grain.—9.* Polygonanthus amazonicus, *lateral view.—10.* Comiphyton gabonense, *polar view. The surface is punctate in the mesocolpia but psilate at the poles and mesocolpial margins.—11.* Sterigmapetalum heterodoxum, *lateral view, psilate surface.—12.* S. obovatum, *portion of a mesocolpium showing a punctate–rugulate surface. Scale bars = 1 μm.*

FIGURES 13–23. *Scanning electron micrographs of Macarisieae pollen.—13.* Macarisia lanceolata, *polar and lateral views. The surface is psilate at the pole and on the margins of the mesocolpia, and punctate–rugulate on the mesocolpia.—14.* M. ellipticifolia, *subpolar view. The surface is psilate and slightly punctate.—15.* M. humbertiana, *lateral view. Surface rugulate, becoming smoother near the colpi.—16.* M. pyramidata, *polar view.—17.* Blepharistemma membranifolia, *lateral view.—18.* Cassipourea afzelii, *lateral view, surface punctate.—19.* C. guianensis, *lateral view. The surface is punctate but not as coarse as in Figure 18.—20.* Dactylopetalum sessiliflorum, *lateral view.—21.* Cassipourea gummiflora *var.* verticillata, *polar view.—22.* Anopyxis kleineana, *lateral view. The surface is psilate; the outline of the large endoaperture is visible.—23.* A. ealeaensis, *lateral view. Scale bars = 1 μm unless otherwise indicated.*

FIGURES 24–35. *Scanning electron micrographs of Rhizophoreae (24–29) and Gynotrocheae (30–35) pollen.—24.* Rhizophora mangle, *lateral view, surface punctate–rugulate.—25.* R. mucronata, *lateral view.—26.* R. stylosa, *lateral view.—27.* Ceriops tagal, *polar view.—28.* Bruguiera gymnorrhiza, *lateral view.—29.* Kandelia candel, *lateral view. Note the outline of the endoaperture.—30.* Gynotroches axillaris, *lateral view. The colpus membrane and the margins of the mesocolpia have a granular–spinulate surface; the rest of the grain has psilate–punctate surface.—31.* Crossostylis grandiflora, *lateral view.—32.* Pellacalyx *cf.* saccardianus, *lateral view.—33.* Carallia eugenioides, *polar view.—34.* C. eugenioides, *lateral view. The surface is psilate–punctate with granular–spinulate mesocolpial margins and colpial membranes.—35.* C. brachiata, *lateral view. Similar to Figure 34 but fewer granules–spinules. Scale bars = 1 μm.*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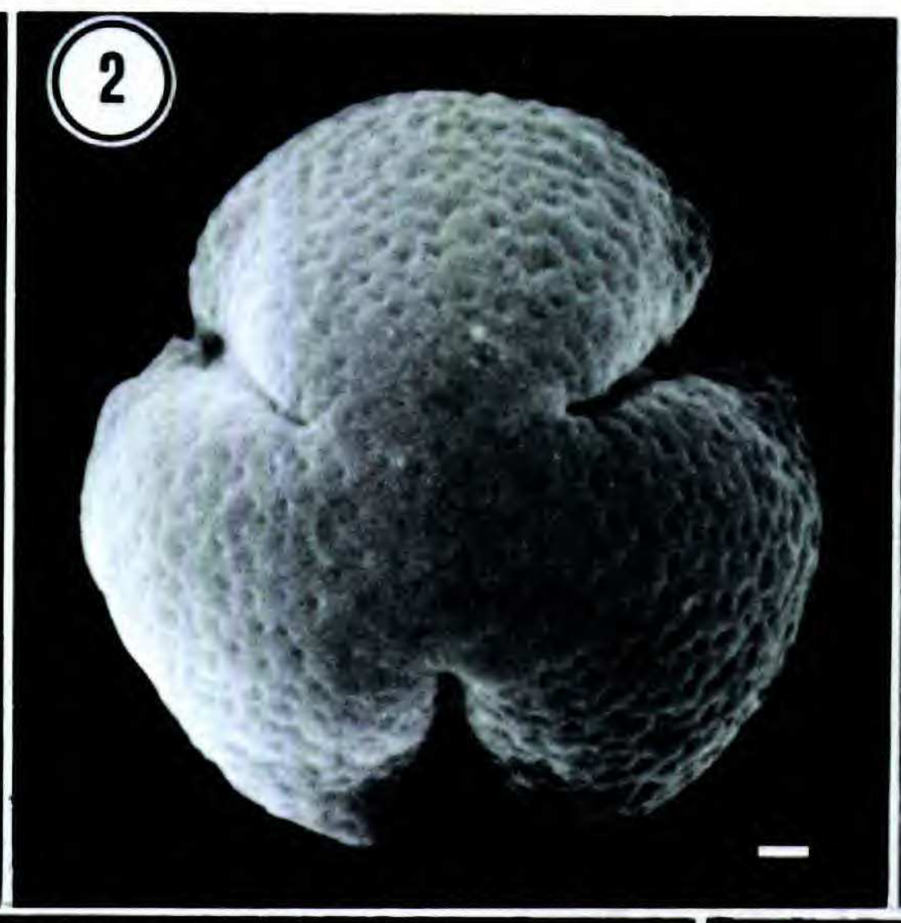
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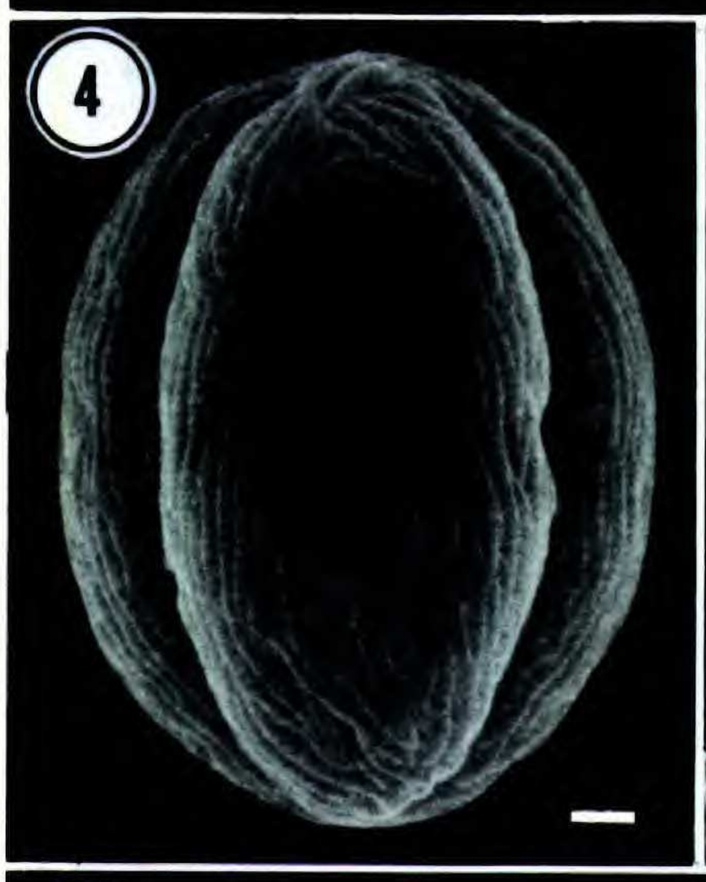
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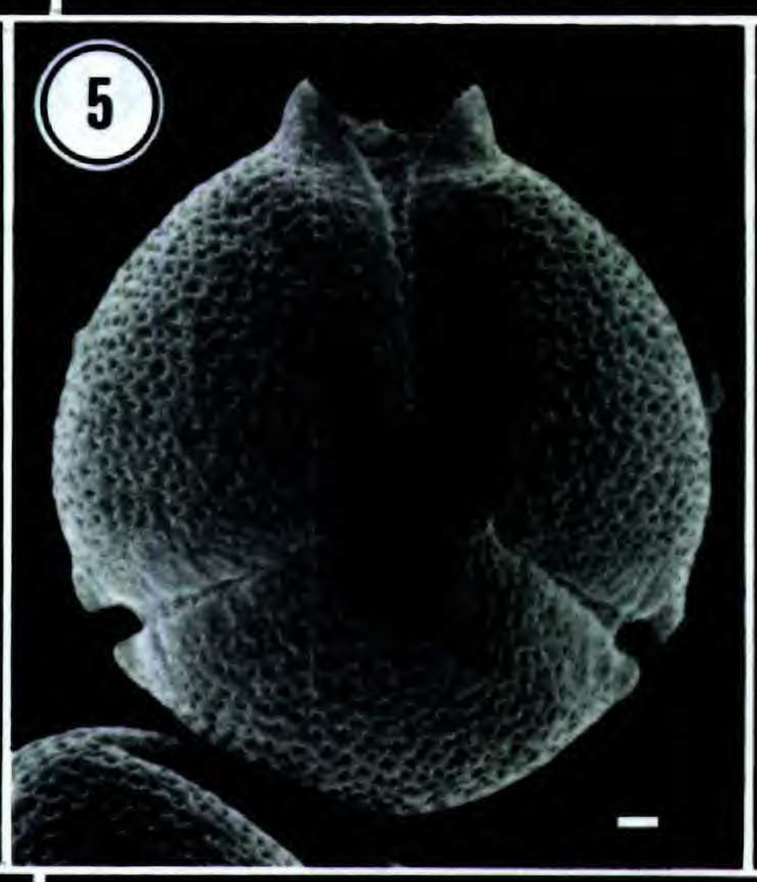
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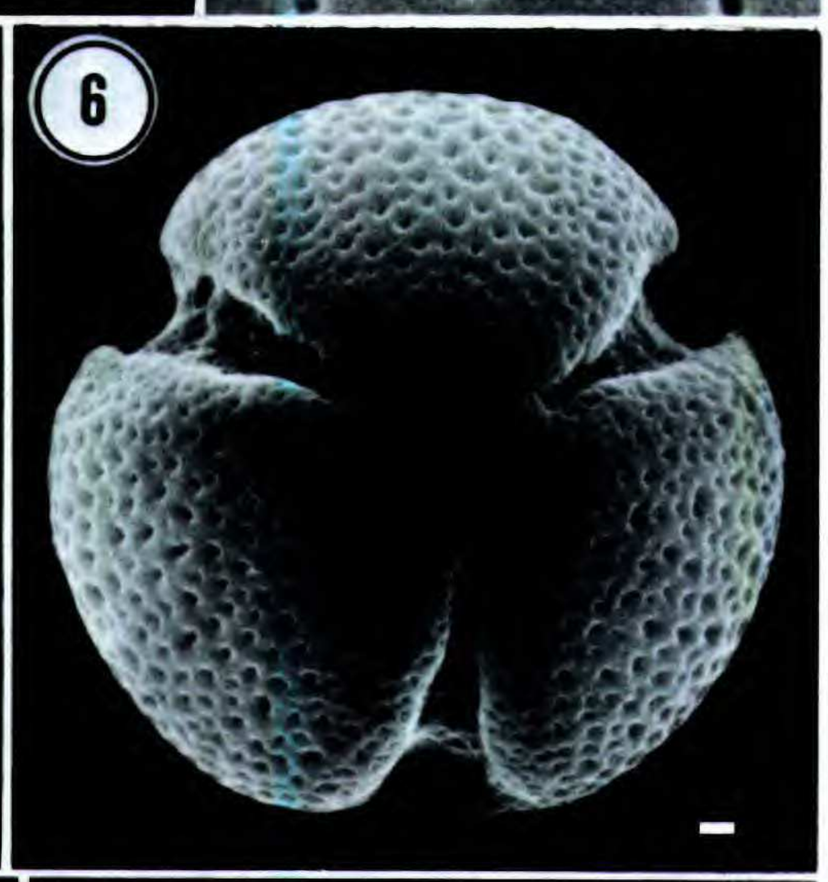
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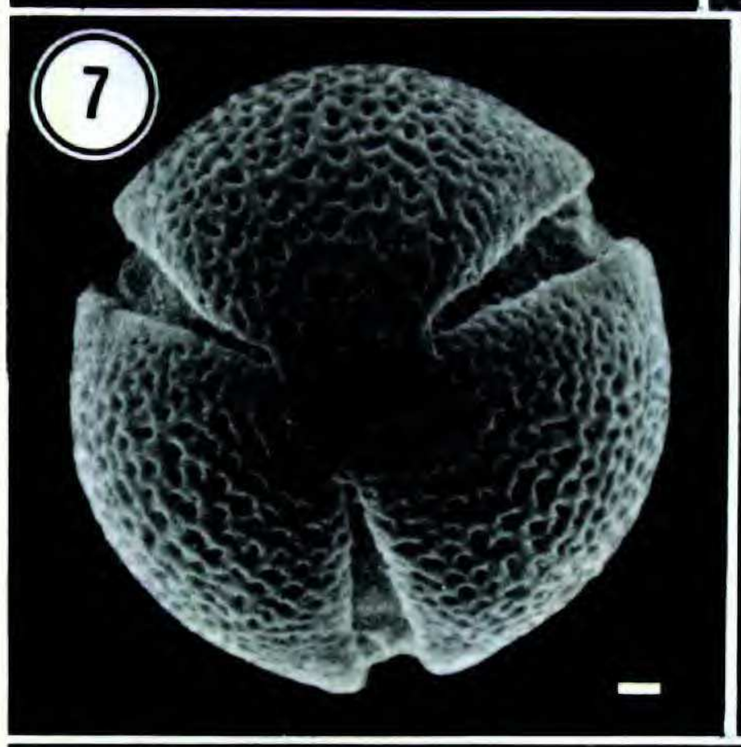
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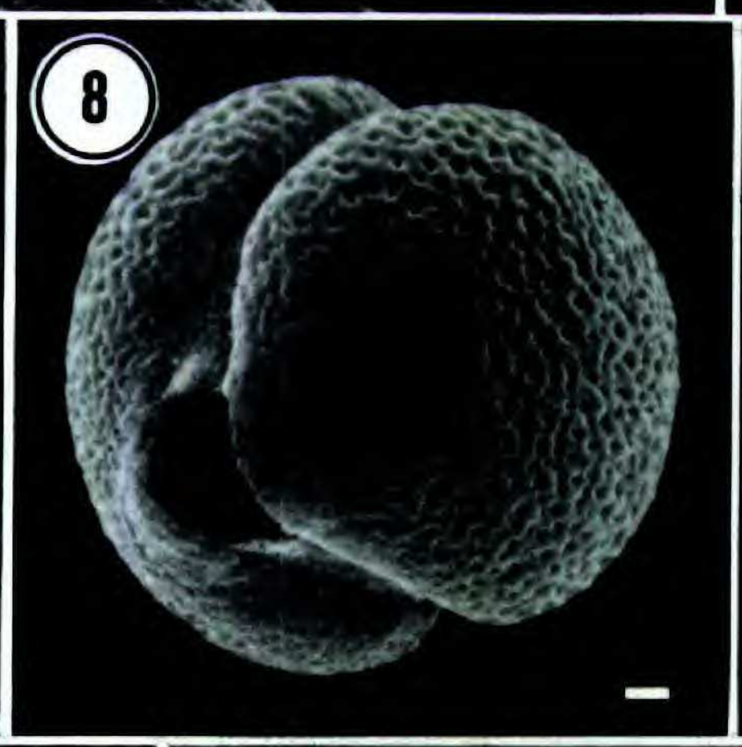
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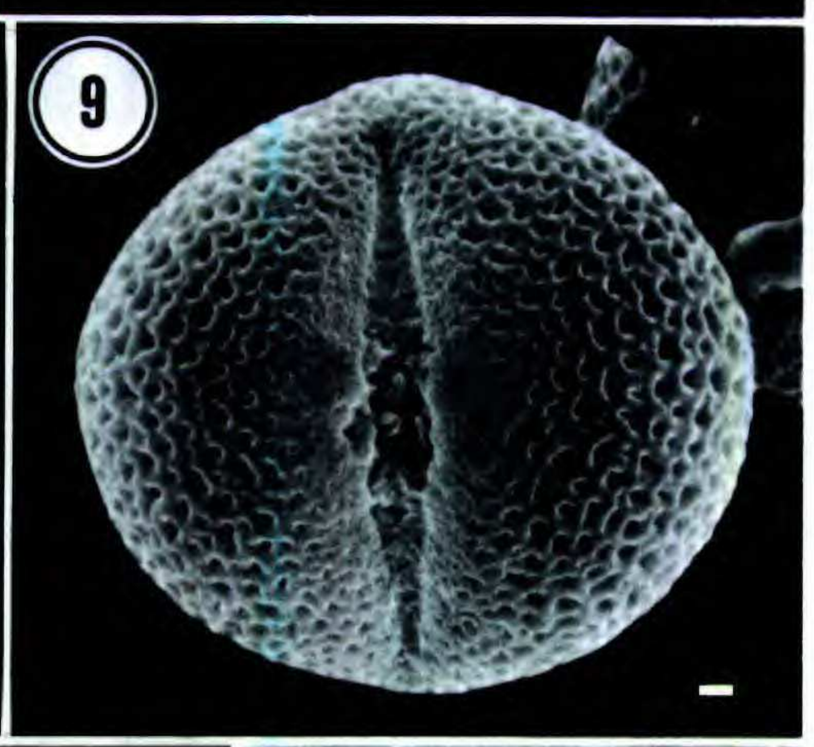
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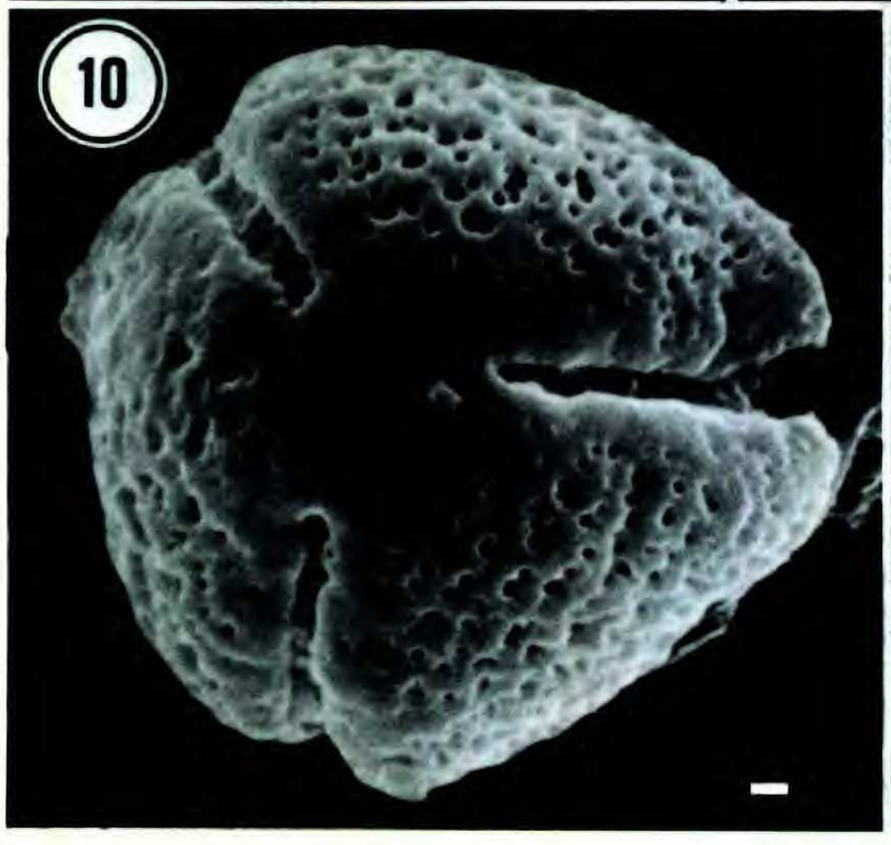
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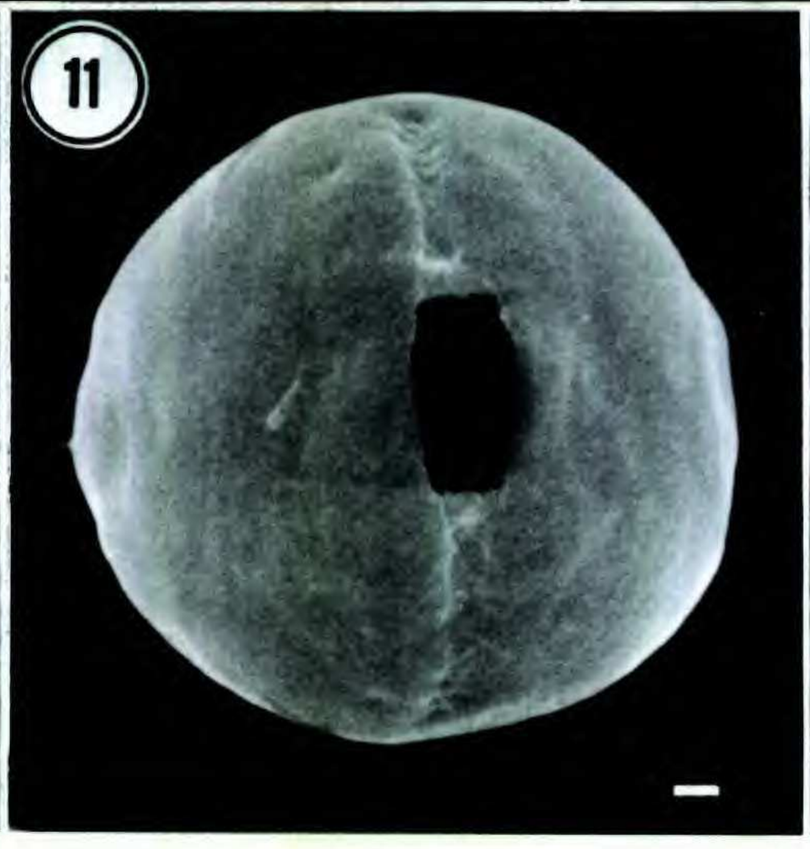
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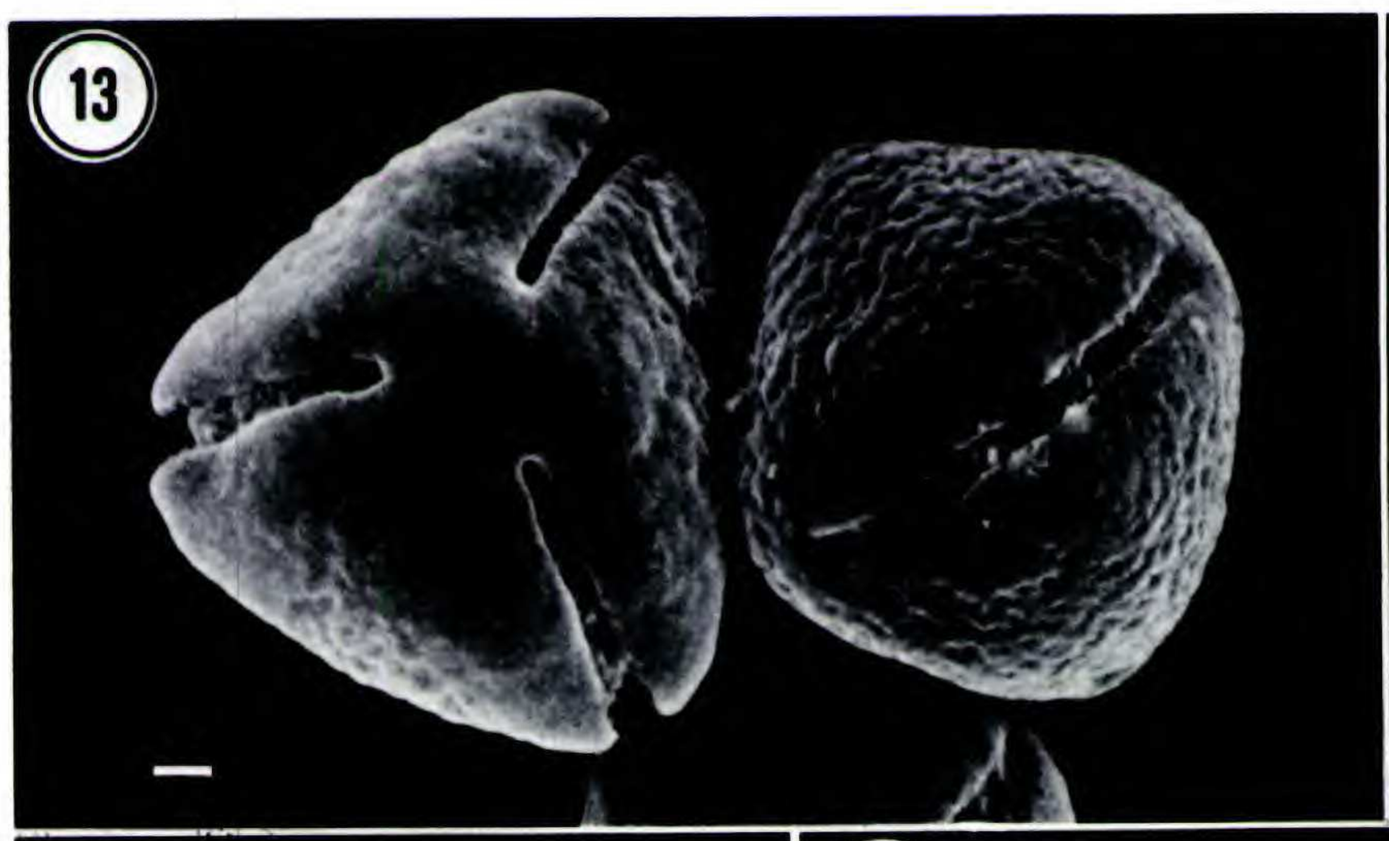
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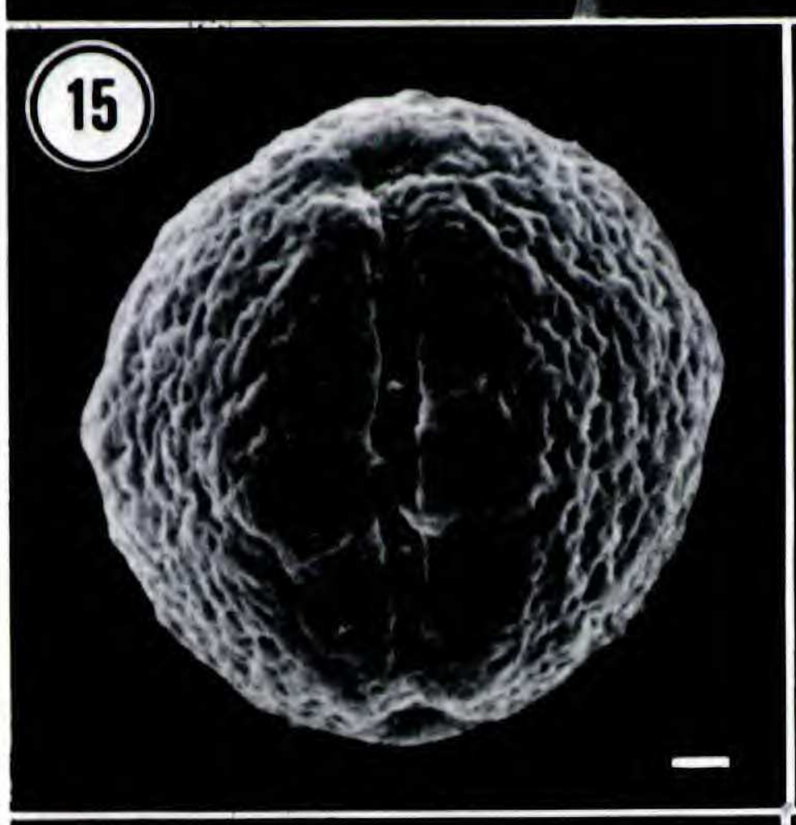
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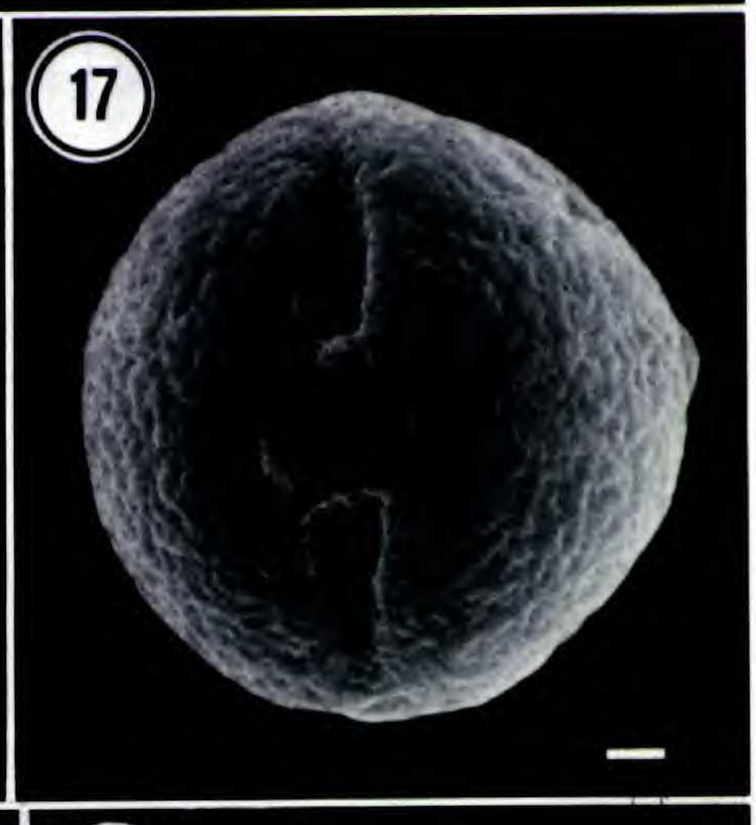
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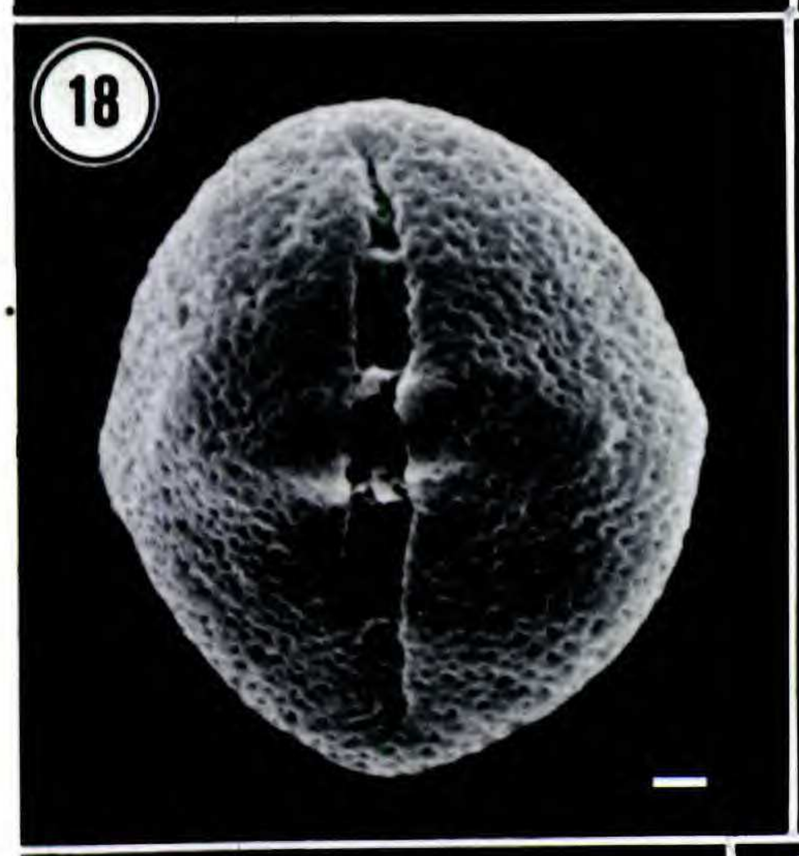
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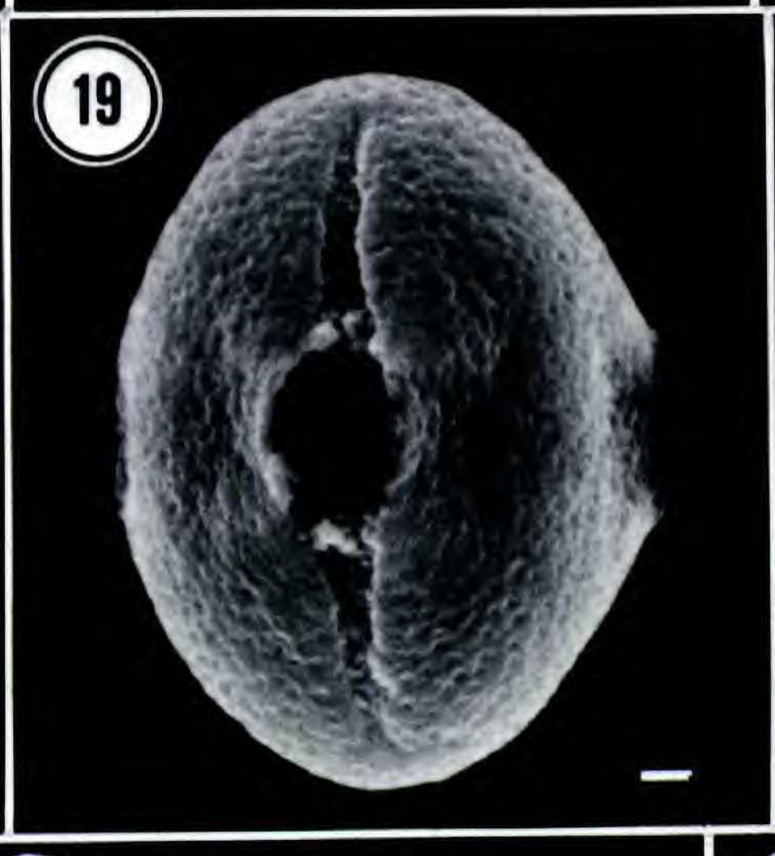
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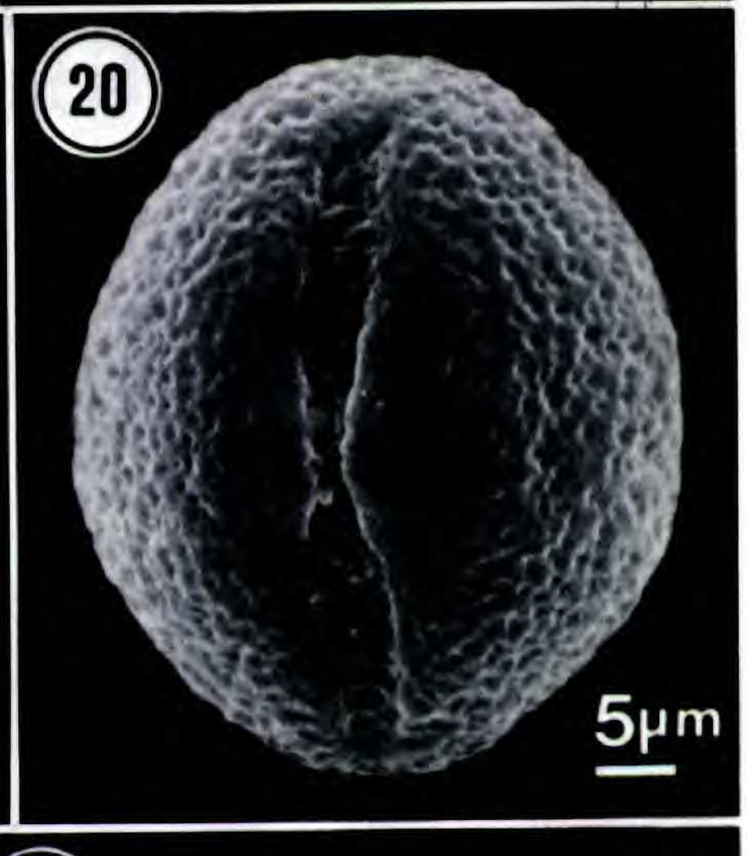
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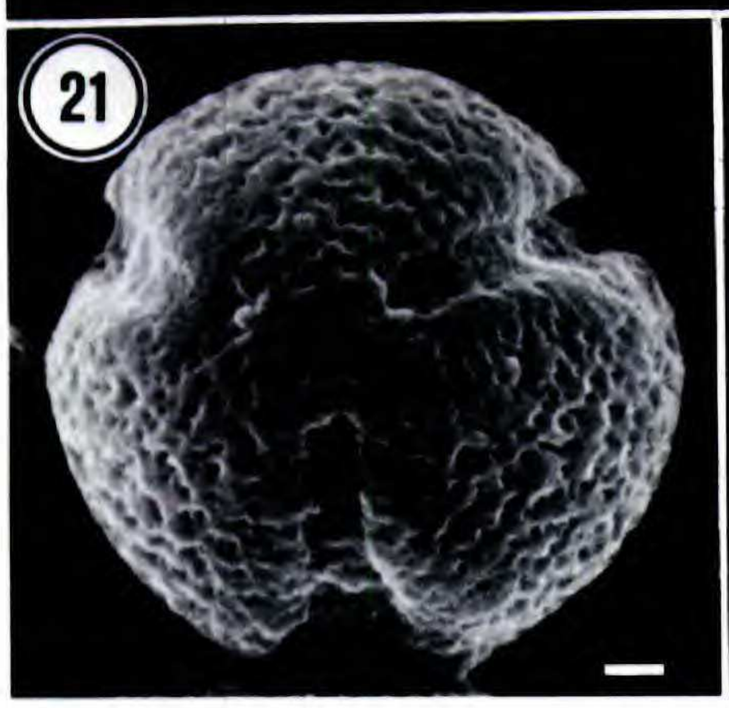
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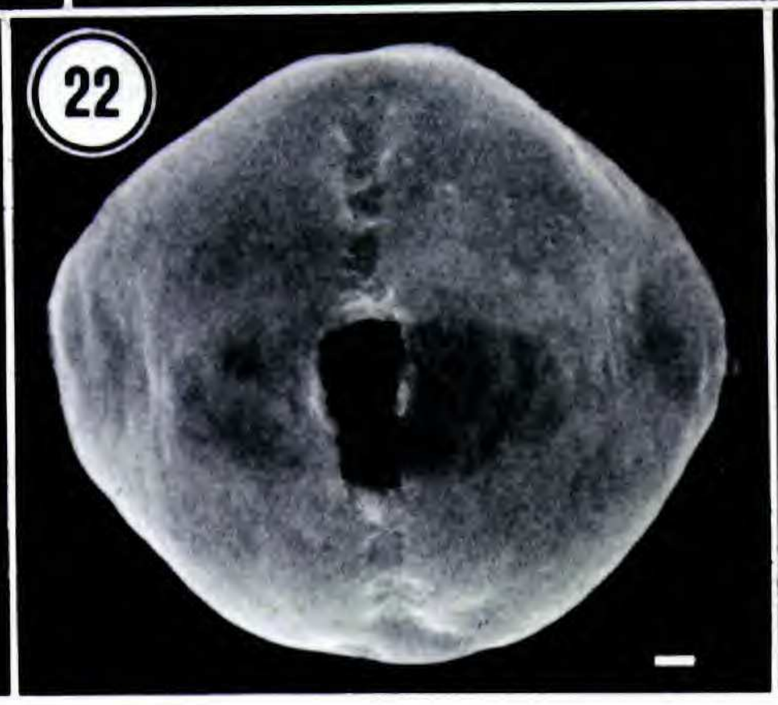
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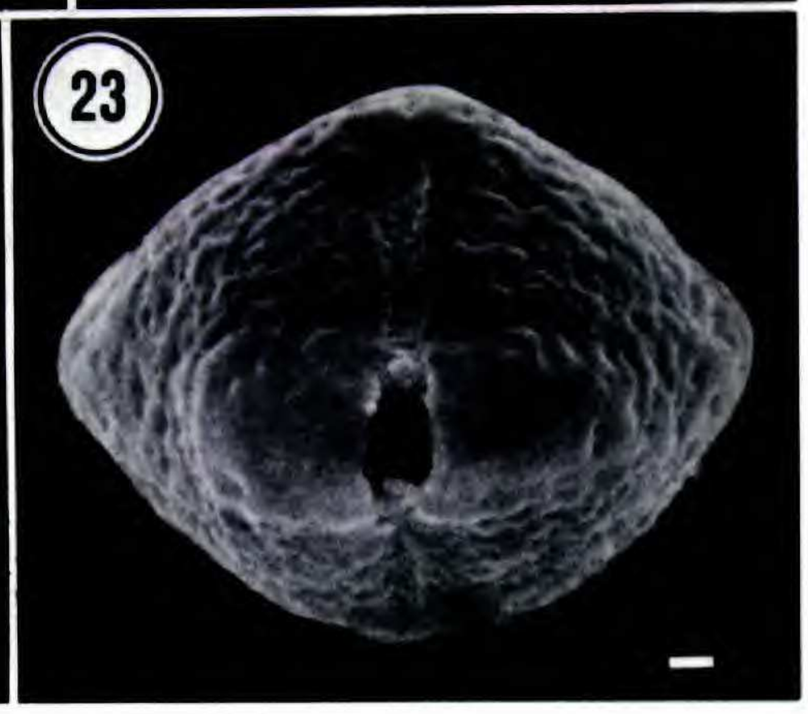
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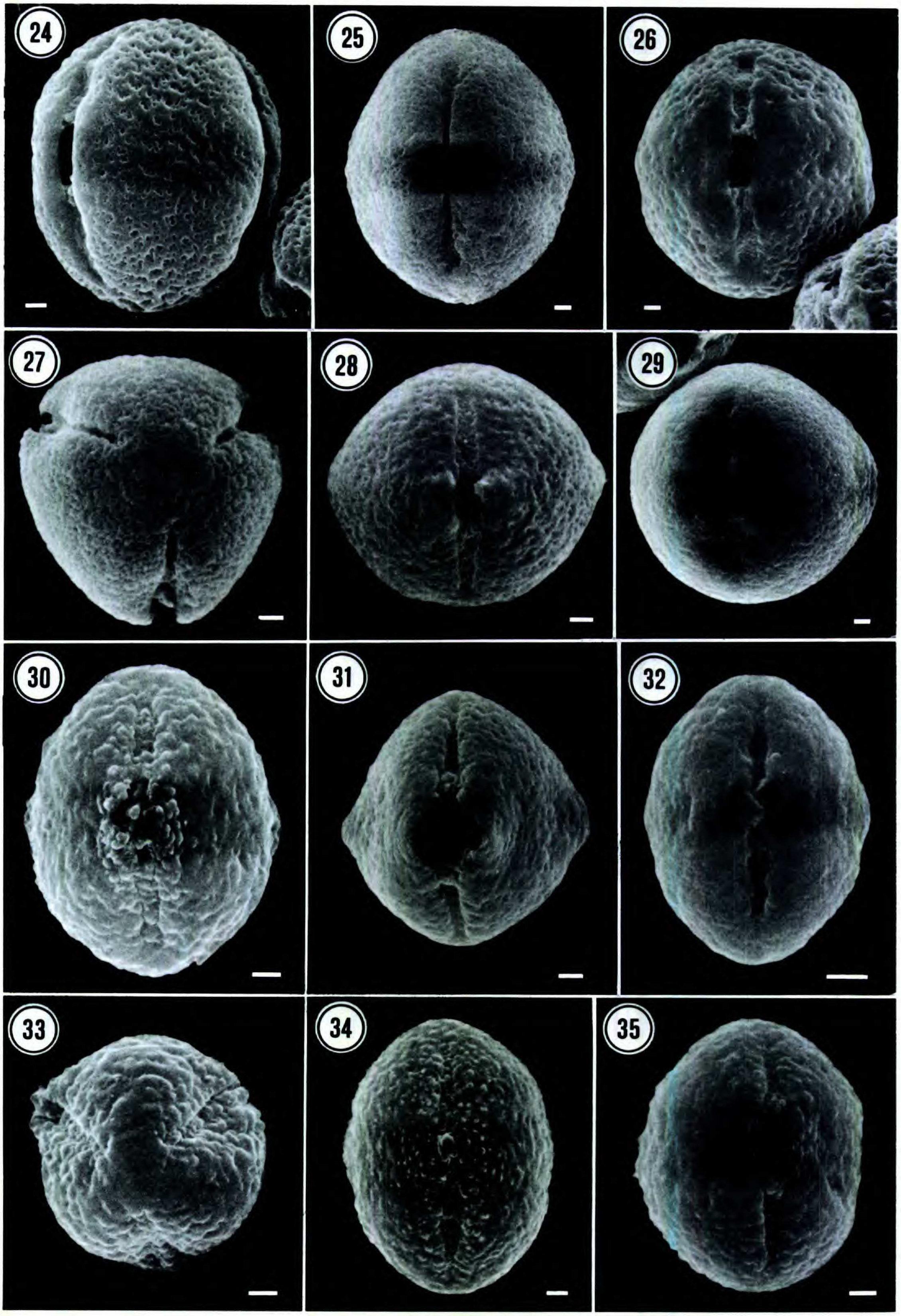
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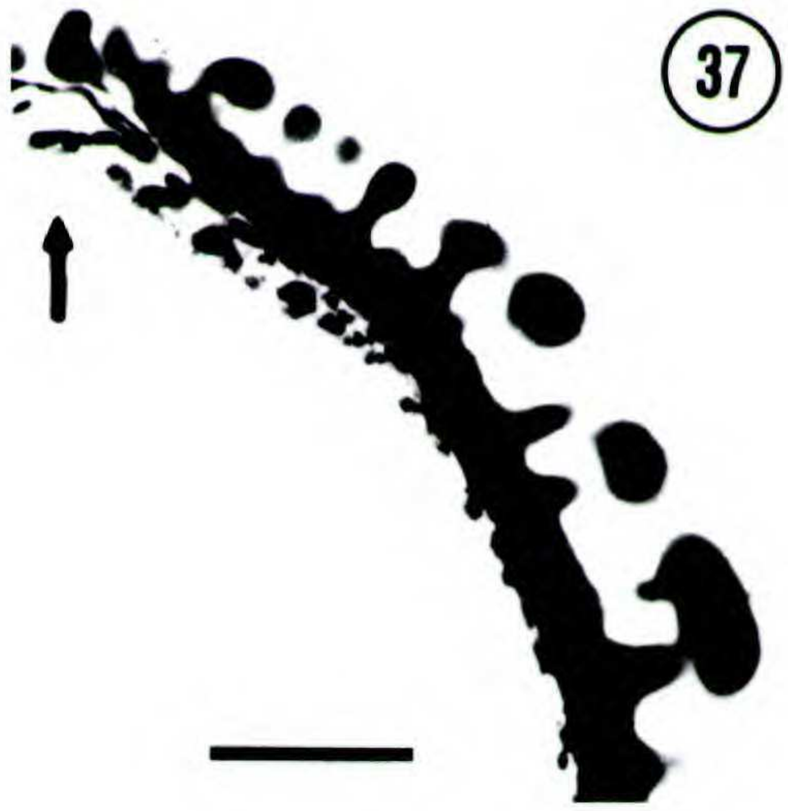
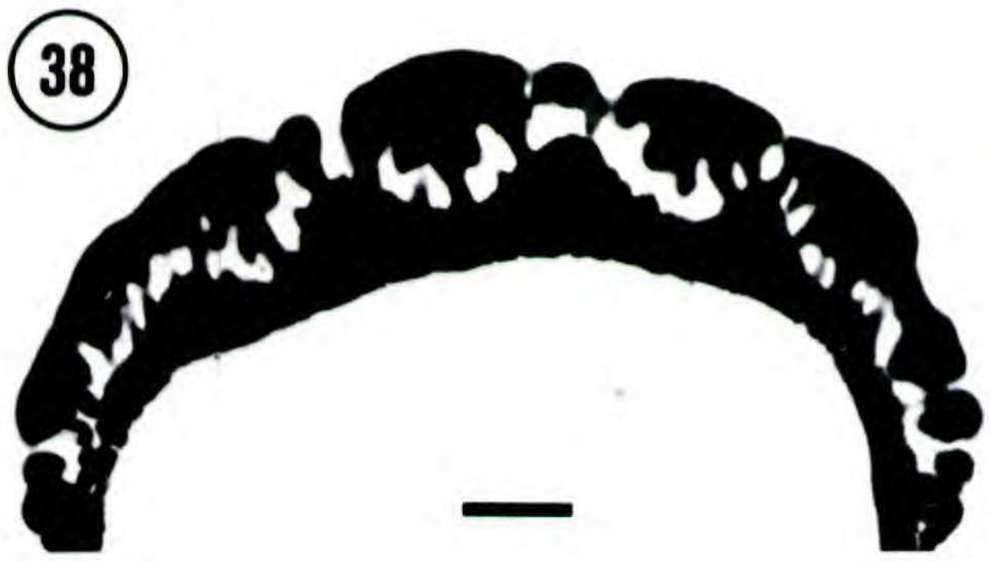
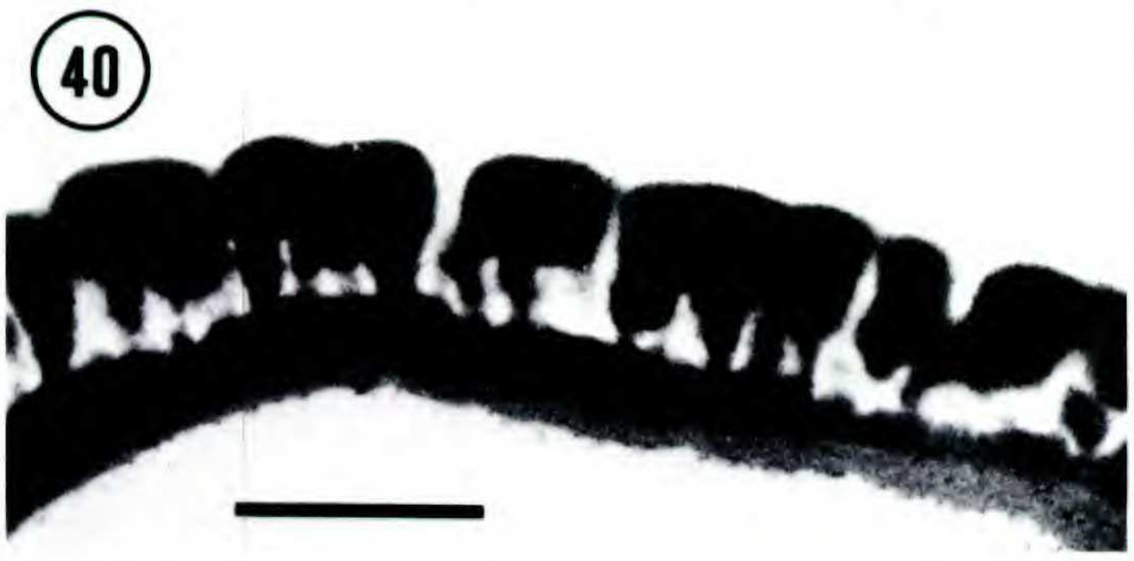
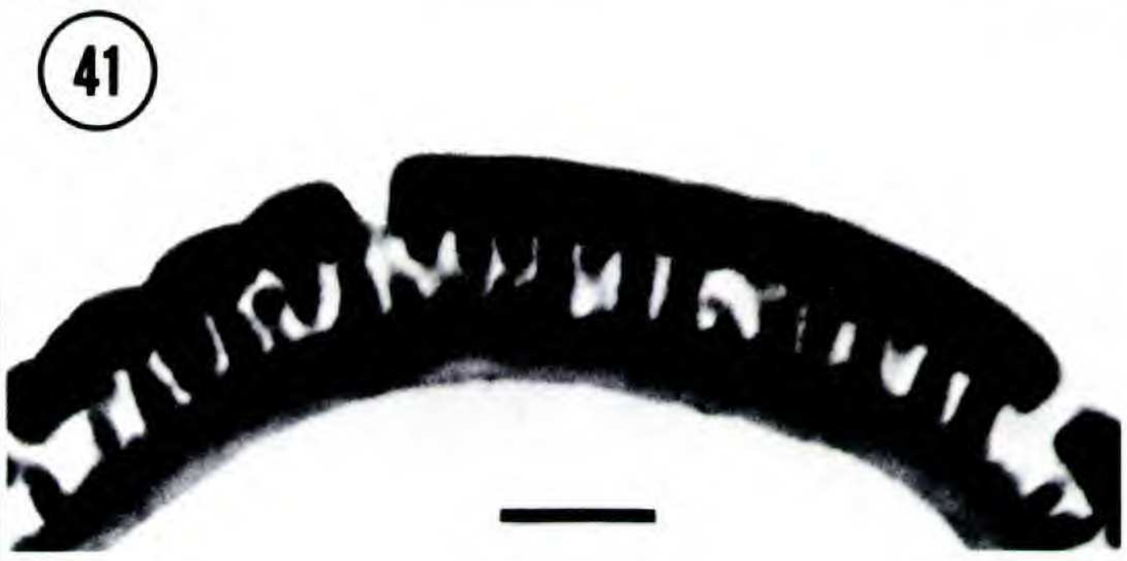
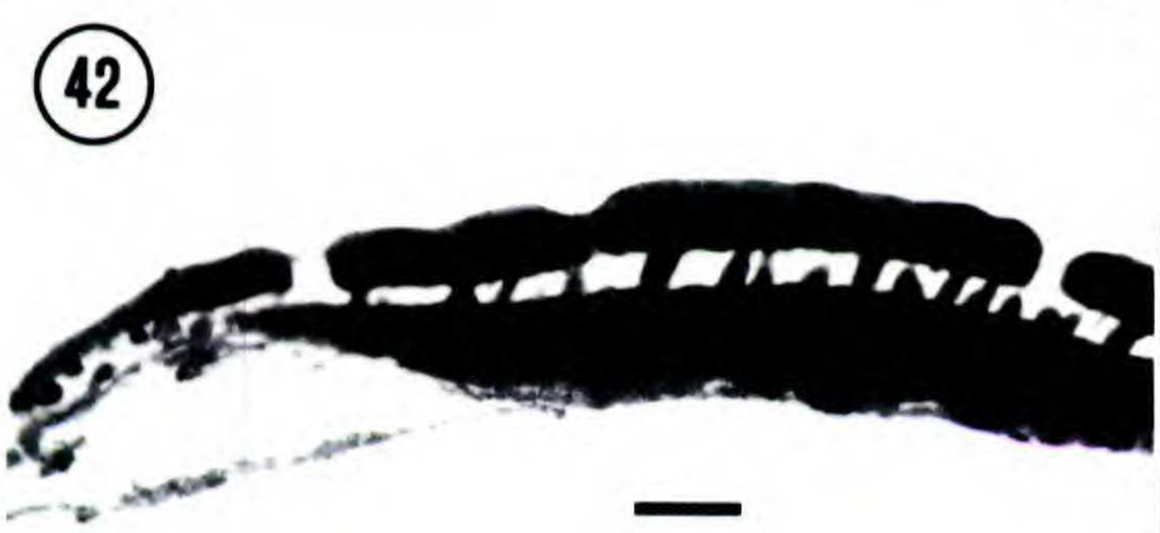
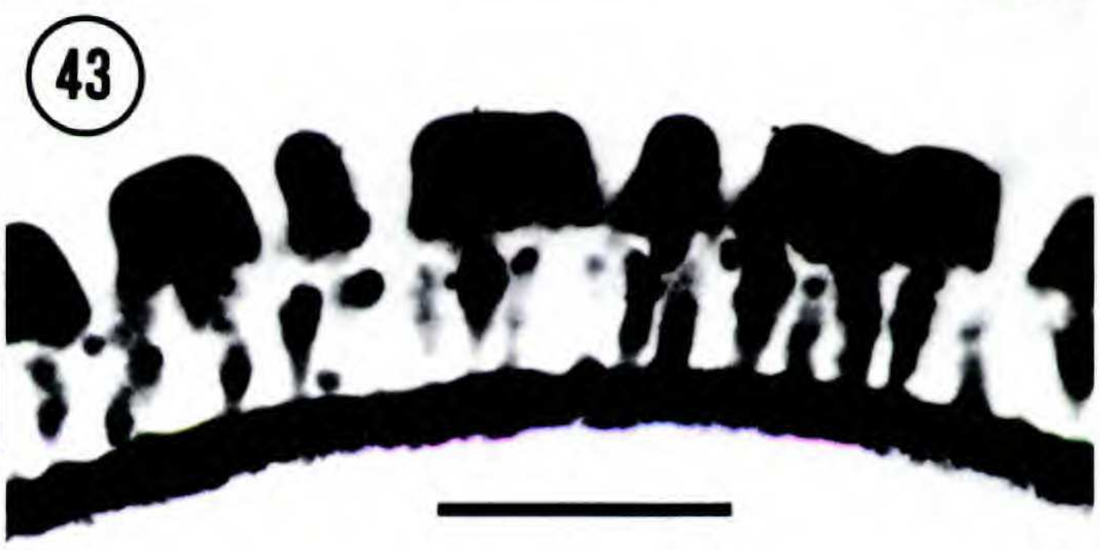




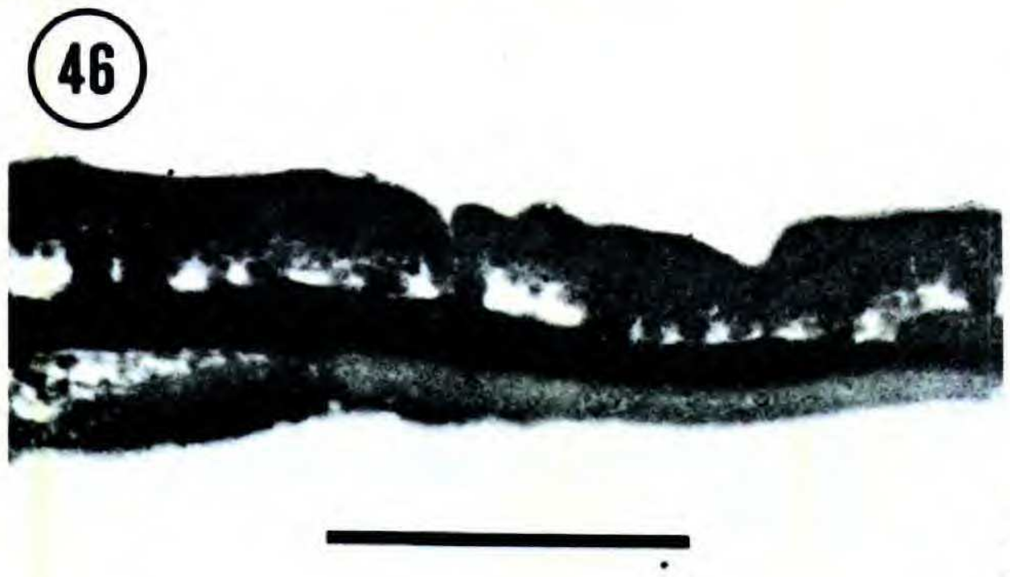


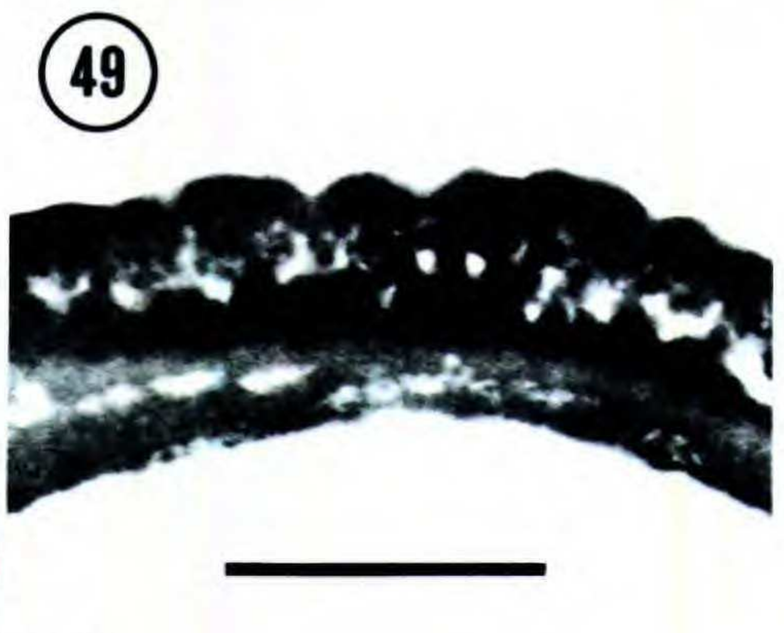


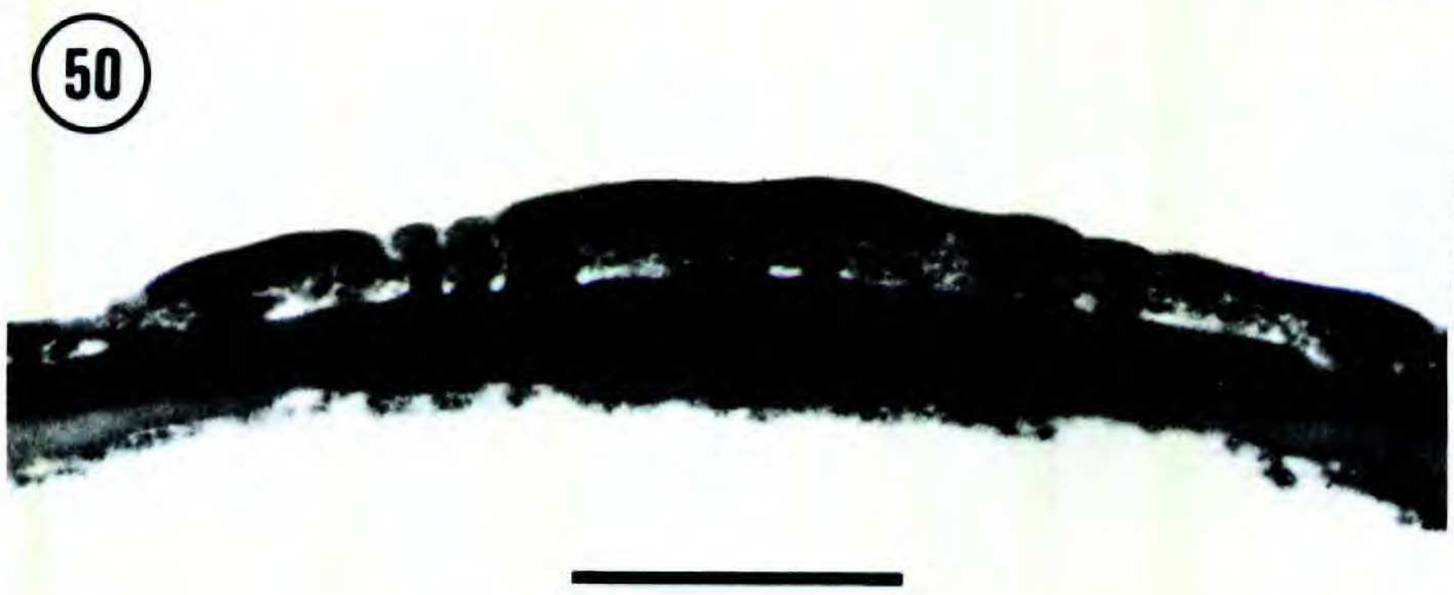


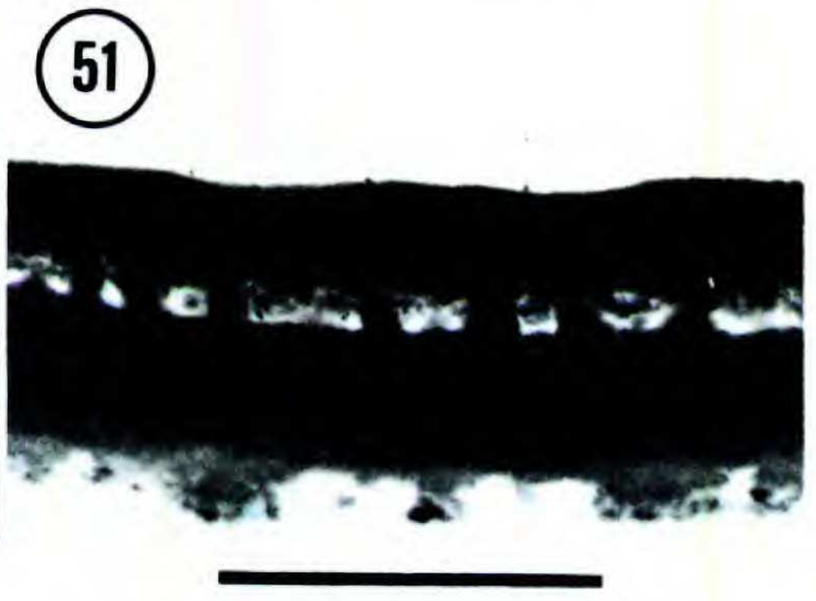


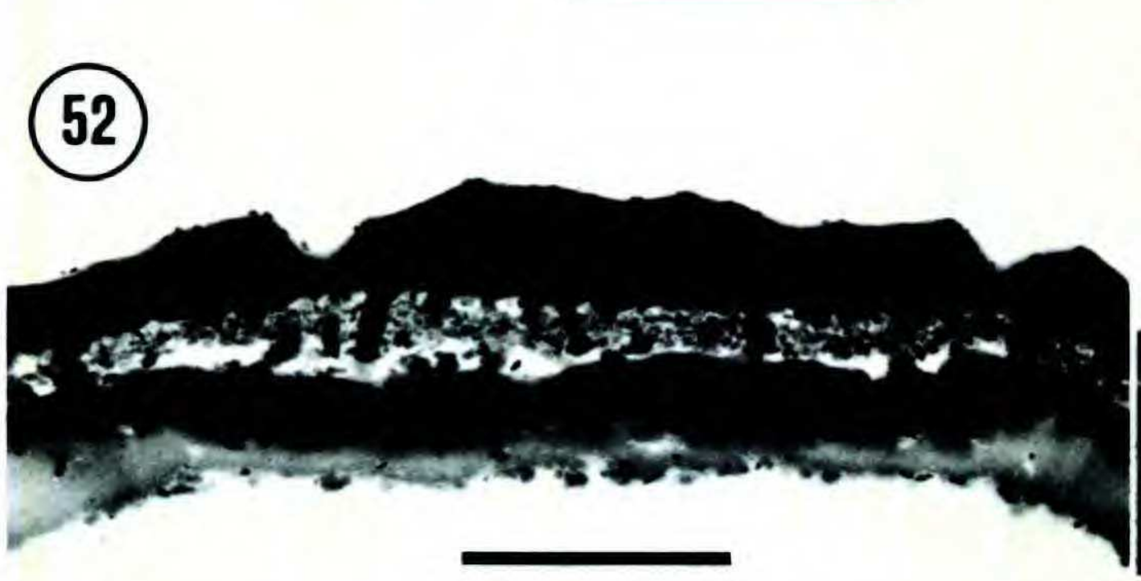
FIGURES 36–43. *Transmission electron micrographs of Anisophylleaceae pollen.—36.* Anisophyllea disticha. *In the center of the mesocolpium the columellae layer is undulating and the corresponding foot layer shows "hills" and "valleys." Toward the colpi the foot layer becomes thin and the columellae are straight. The outer margin of the tectum appears lobed due to perpendicularly sectioned striae.—37.* Combretocarpus rotundatus. *Section of a mesocolpium near an endoaperture (arrow). The tectum is incomplete, the columellae simple, the foot layer uniform, and the endexine disrupted.—38, 39.* Anisophyllea obtusifolia. *The undulating columellae (as in Fig. 38) are present only in some areas of the grain, possibly near the equator. In other sections, the middle part of the mesocolpium also has straight columellae (as in Fig. 39, to the left).—40.* A. fallax. *The tectum is thick and incomplete, the columellae thin and short, and the foot layer and endexine uniform.—41.* A. laurina. *The columellae are well developed.—42.* Polygonanthus amazonicus. *The foot layer is thick and tapering toward the endoaperture (left).—43.* Poga oleosa. *The tectum is incomplete and thick; the columellae are tall, becoming granular distally; the foot layer is thin; and the endexine is thicker than the foot layer and is uniform. Scale bars = 1 μm.*

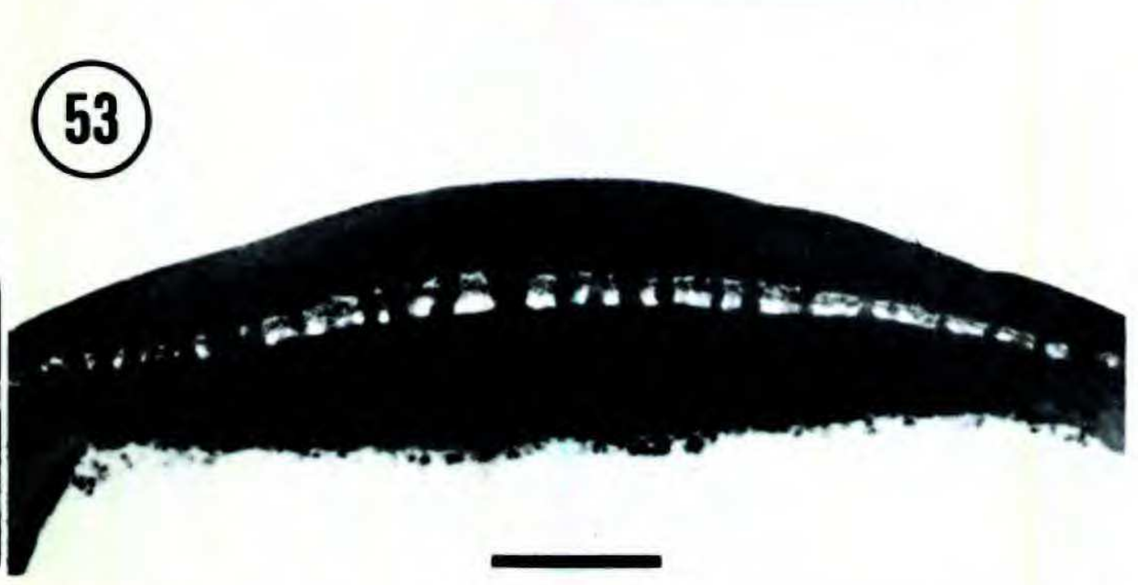












FIGURES 44–53. *Transmission electron micrographs of Gynotrocheae (44–49) and Macarisieae (50–53) pollen.—44.* Carallia brachiata *and 45.* C. eugenioides. *In both, the tectum is thin, the columellae are short and unbranched, the foot layer is uneven in thickness and the endexine is uniform but has long, narrow gaps in Figure 44.—46.* Crossostylis grandiflora. *A thin granular layer is present just below the tectum. The endexine is thicker and has irregular open spaces near a colpus (left).—47.* Gynotroches axillaris. *The exine is similar to that in* Carallia.—*48.* Pellacalyx pustulata. *The tectum is thin, the short columellae are extensively branched, and the foot layer is thin and irregular. A line separates the foot layer from the endexine. The latter becomes very thick near the colpus, where it has a large, irregular gap.—49.* P. *cf.* saccardianus. *The exine is similar*

Discussion

Lack of endoaperture fusion is the only feature of Anisophylleaceae pollen that does not overlap variation within Rhizophoraceae. Therefore, the phenetic gap between the two families results from the combined effects of many characters. With LM, for example, Anisophylleaceae OTUs have the highest or lowest average (or median) in 8 of 10 characters (1, 2, 4–8, and 10) and the same high average as Rhizophoreae for character 3. Anisophylleaceae OTUs also have the highest or lowest average for six TEM characters (24–26, 29–31) and the second highest average for characters 27 and 28. Also with TEM, Anisophylleaceae pollen can be separated from Gynotrocheae by a much lower endexine thickness ratio, and from Macarisieae by lack of intercolumellar granulation.

SEM analysis reveals the punctate-only sculpture of four Anisophylleaceae OTUs. *Combretocarpus rotundatus* (A4) differs slightly by having psilate mesocolpial margins. The striate sculpture of *Anisophyllea disticha* (A1) is strikingly different from any other in this study and is primarily responsible for isolating *A. disticha* along component III. In contrast, punctate pollen within Rhizophoraceae is usually psilate–punctate or punctate–rugulate. Exceptions include *Cassipourea elliptica* (M3), which is punctate-only, and *Dactylopetalum sessiliflorum* (M5), which has the same SEM character states as *C. rotundatus* (A4). The similarity in exine sculpture between *D. sessiliflorum* and *C. rotundatus* partially accounts for their connection on the minimum spanning tree.

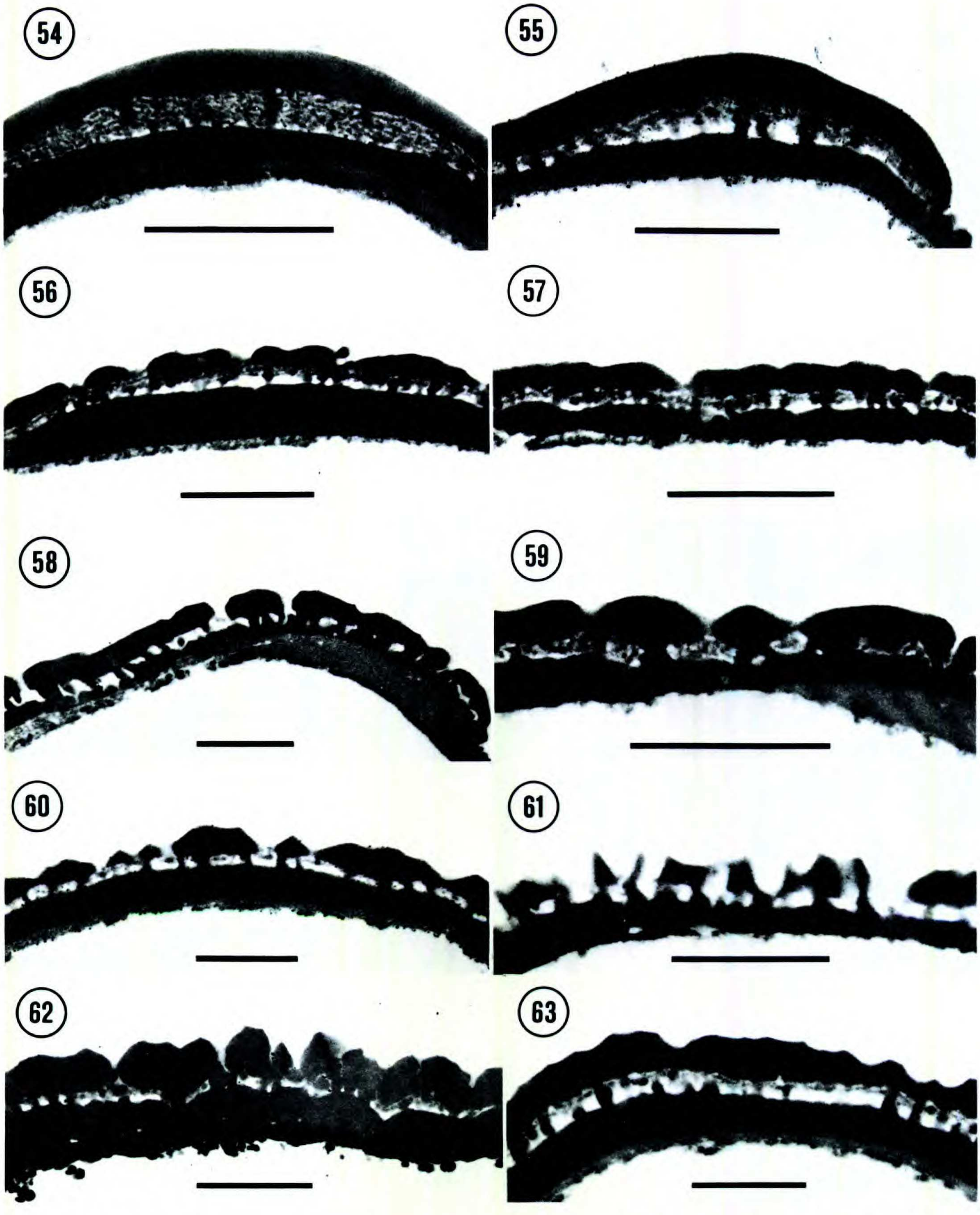
Pollen of Anisophylleaceae can therefore be distinguished from Rhizophoraceae by the following combination of character states: larger polar axis and breadth, greater variation in polar axis and breadth, higher P/E ratio (in the subprolate–prolate range), narrow or nonexistent endoapertures, lack of endoaperture fusion, relatively small polar area (including some syncolpate grains), punctate sculpture, thicker tectum, taller and wider columellae, the highest tectum thickness and columellae height ratios, the lowest foot layer ratio, a low endexine ratio, and absence of intercolumellar granulation. These results agree with separate familial status for Anisophylleaceae. On the other hand, Anisophylleaceae, even without *Anisophyllea disticha* (A1), is a relatively variable taxon with longer average links on the minimum spanning tree than the tribes of Rhizophoraceae.

Pollen of Gynotrocheae, Macarisieae, and Rhizophoreae can be generally characterized, but these tribes cannot be separated based on palynological evidence. Characteristics generally distinguishing pollen grains of Rhizophoreae from those of Macarisieae and Gynotrocheae are larger size, lower P/E ratios (averaging 100), greater distances between colpal ends, higher polar area indexes, punctate–rugulate sculpture, thicker tecta, taller and wider columellae, and thicker foot layers. At the opposite end of the continuum are Gynotrocheae with the smallest grains, highest P/E ratios (average 119), psilate–punctate sculpture, highest endoapertural indexes, lowest foot layer ratios, and highest endexine ratios. Results of the phenetic analysis are not consistent with the proposed separation of *Crossostylis grandiflora* (G3) from Gynotrocheae (see other symposium papers, this volume). In both the ordination and minimum spanning tree, *C. grandiflora* is located within the group of Gynotrocheae OTUs.

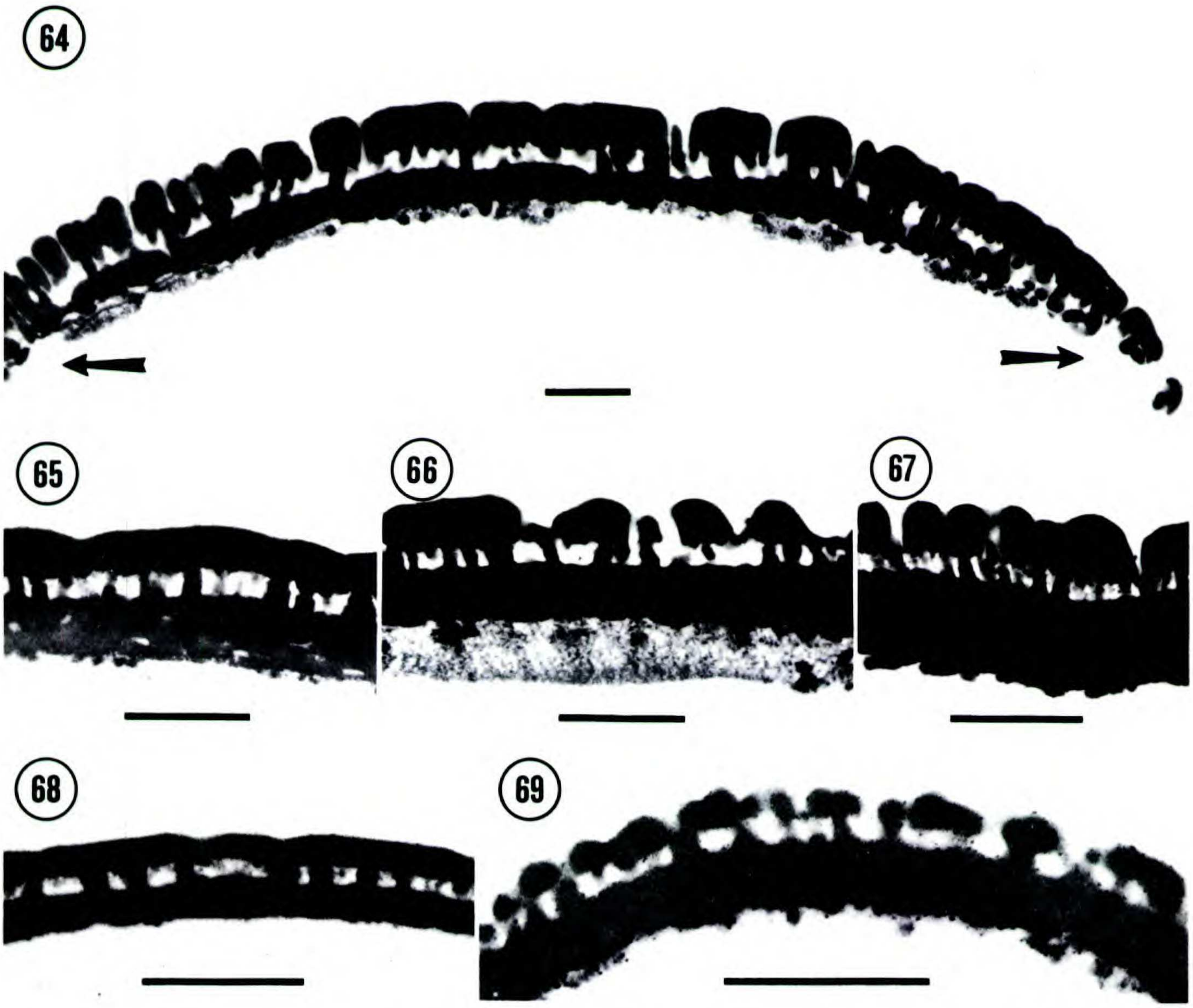
Macarisieae OTUs are widely distributed in phenetic space, partly because of the many exceptions to the predominant SEM character states. There is essentially no phenetic gap between Macarisieae and either Rhizophoreae or Gynotrocheae. Macarisieae is also most similar to Anisophylleaceae. In many measurements and ratios, the Macarisieae average is between Rhizophoreae and Gynotrocheae, including polar axis and breadth, P/E ratio, distance between colpal ends, polar area index, tectum and foot layer thickness, height and width of columellae, columellar height ratio, and foot layer and endexine thickness ratios. Macarisieae pollen is also characterized by the presence of intercolumellar granulation. Only two OTUs outside Macarisieae, *Crossostylis grandiflora* (G3) and *Pellacalyx* cf. *saccardianus* (G5), have this feature, and only one Macarisieae OTU, *Cassipourea elliptica* (M3), lacks granulation.

←

to that in Figure 48 but no line is evident.—50. Anopyxis ealeaensis. *The narrow columellae layer has a granular matrix. The foot layer is very thick.—51.* A. kleineana. *The exine is similar to that of the previous species, but the endexine is highly disrupted.—52.* Sterigmapetalum obovatum. *The granular matrix is well developed, and the columellae are cut obliquely.—53.* S. heterodoxum. *The distinct granular layer is present below the tectum. The foot layer is very thick; the endexine is thin and disrupted in the mesocolpium but is well developed below the colpi. Scale bars = 1 μm.*



FIGURES 54–63. *Transmission electron micrographs of Macarisieae pollen.*—*54.* Macarisia lanceolata. *Middle part of a mesocolpium. Note that the intercolumellar spaces are filled with a granular matrix.*—*55.* M. ellipticifolia. *Mesocolpium near a colpus (on the right).*—*56.* M. humbertiana. *Foot layer quite thick, and endexine granular due to proximity of circular endoaperture.*—*57.* M. pyramidata. *In 55, 56, and 57 the granular layer (matrix) is not as extensive as in 54.*—*58.* Cassipourea elliptica. *An oblique section showing part of a mesocolpium near a colpus (to the right). Here the endexine is greatly thickened and is granular on the left due to the proximity of an endoaperture.*—*59.* Blepharistemma membranifolia. *Granular matrix present, endexine thin or absent except near the colpus, where it is very thick (to the right).*—*60.* Dactylopetalum sessiliflorum. *Middle part of a mesocolpium; a thin granular layer below the tectum.*—*61.* D. zenkeri. *Incomplete tectum suggests a reticulate or meshlike surface.*—*62.* Comiphyton gabonense. *Columellae layer is narrow and has some granules below the tectum.*—*63.* Petalodactylis obovata. *Exine similar to those in 55, 56, and 57. Scale bars = 1 μm.*



FIGURES 64–69. *Transmission electron micrographs of Rhizophoreae pollen.—64.* Rhizophora mucronata (9947), section of an entire mesocolpium. Tectum incomplete, columellae simple, and foot layer uniform. Endexine is granular in the mesocolpium, probably due to the vicinity of the circular, fused endoapertures. Near the open endoapertures (arrows) the foot layer and endexine are absent.—65. R. stylosa. *Tectum complete; endexine very thick.—66.* R. mangle. *Tectum incomplete in some areas; the thick granular endexine is probably due to the circular endoaperture.—67.* Kandelia candel. *Note the massive endexine. Columellae appear to become granular distally.—68.* Bruguiera gymnorrhiza. *A few granules, similar to those described for Macarisieae, are present in the intercolumellar spaces. The thin endexine is difficult to distinguish.—69.* Ceriops tagal. *Tectum incomplete, foot layer very thick, and endexine thin and disrupted. Scale bars = 1 μm.*

CONCLUSION

Principal components analysis using palynological data clearly separates Anisophylleaceae from Rhizophoraceae and supports the hypothesis of separate familial status for Anisophyllaceae. If Macarisieae pollen data were not considered, Rhizophoreae and Gynotrocheae OTUs would also form discrete phenetic groups. Including Macarisieae pollen data changes this picture to one of continuous phenetic variation from Rhizophoreae through Macarisieae to Gynotrocheae.

The majority of pollen morphological characteristics in Anisophylleaceae and Rhizophoraceae occur in a broad range of families throughout the angiosperms. Therefore, it was not possible within the limits of this study to suggest relationships with other taxa. It seems particularly significant that neither family we investigated can be connected to Myrtales on palynological grounds. Light and ultrastructural data on Myrtales pollen (Patel et al., 1985) are generally comparable to data in this study. The colporoidate or fused endoapertures possessed by Anisophylleaceae or Rhizophoraceae have no counterpart in Myrtales, however, and the pseudocolpi of Myrtales pollen do not correspond to features of either Anisophylleaceae or Rhizophoraceae pollen.

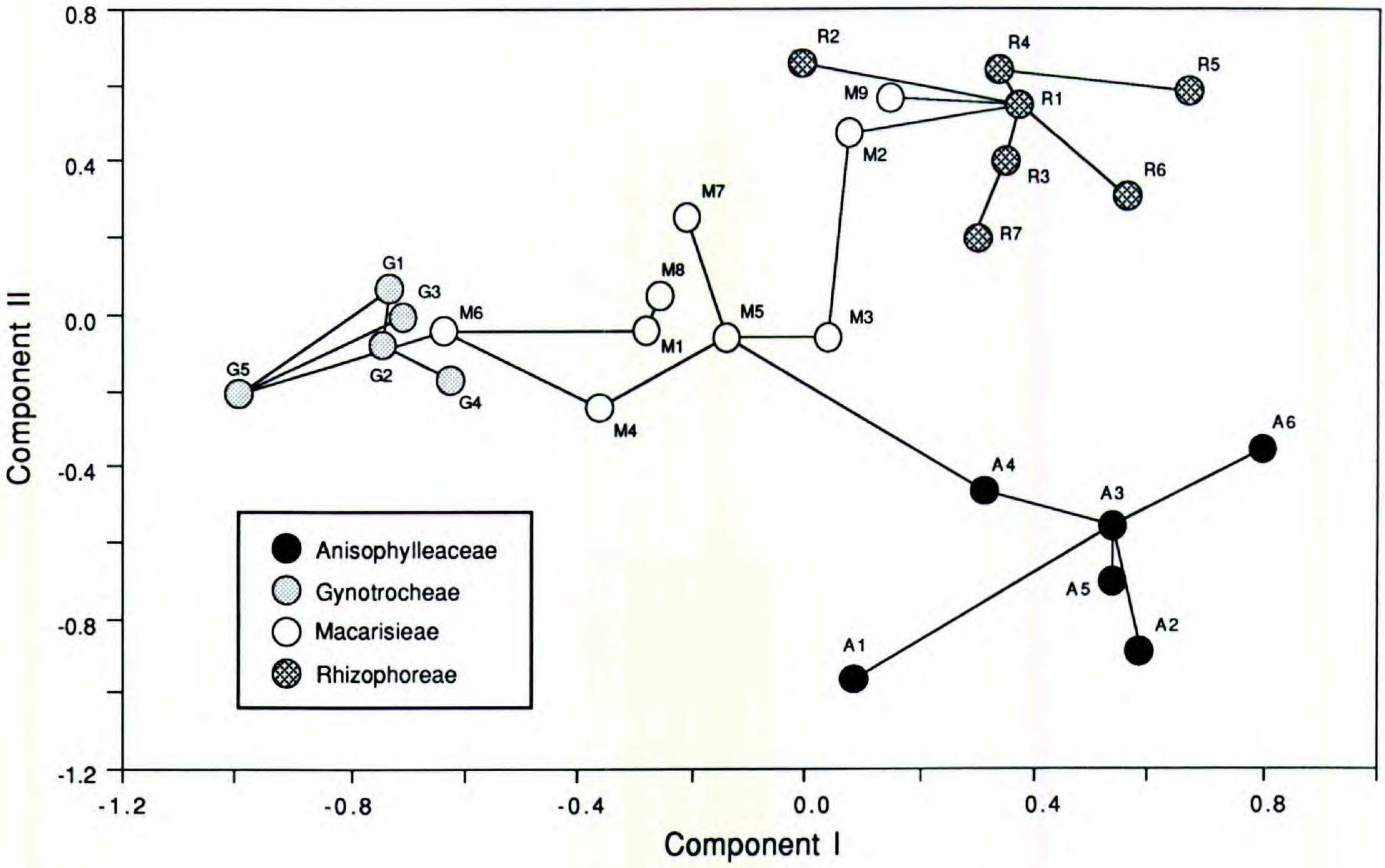


FIGURE 70. *Projection of 27 OTUs onto the first two principal components (data from Table 3). Percent of total variation explained is 25.5 for component I and 20.7 for component II. The superimposed minimum spanning tree was calculated from an average taxonomic distance matrix.*

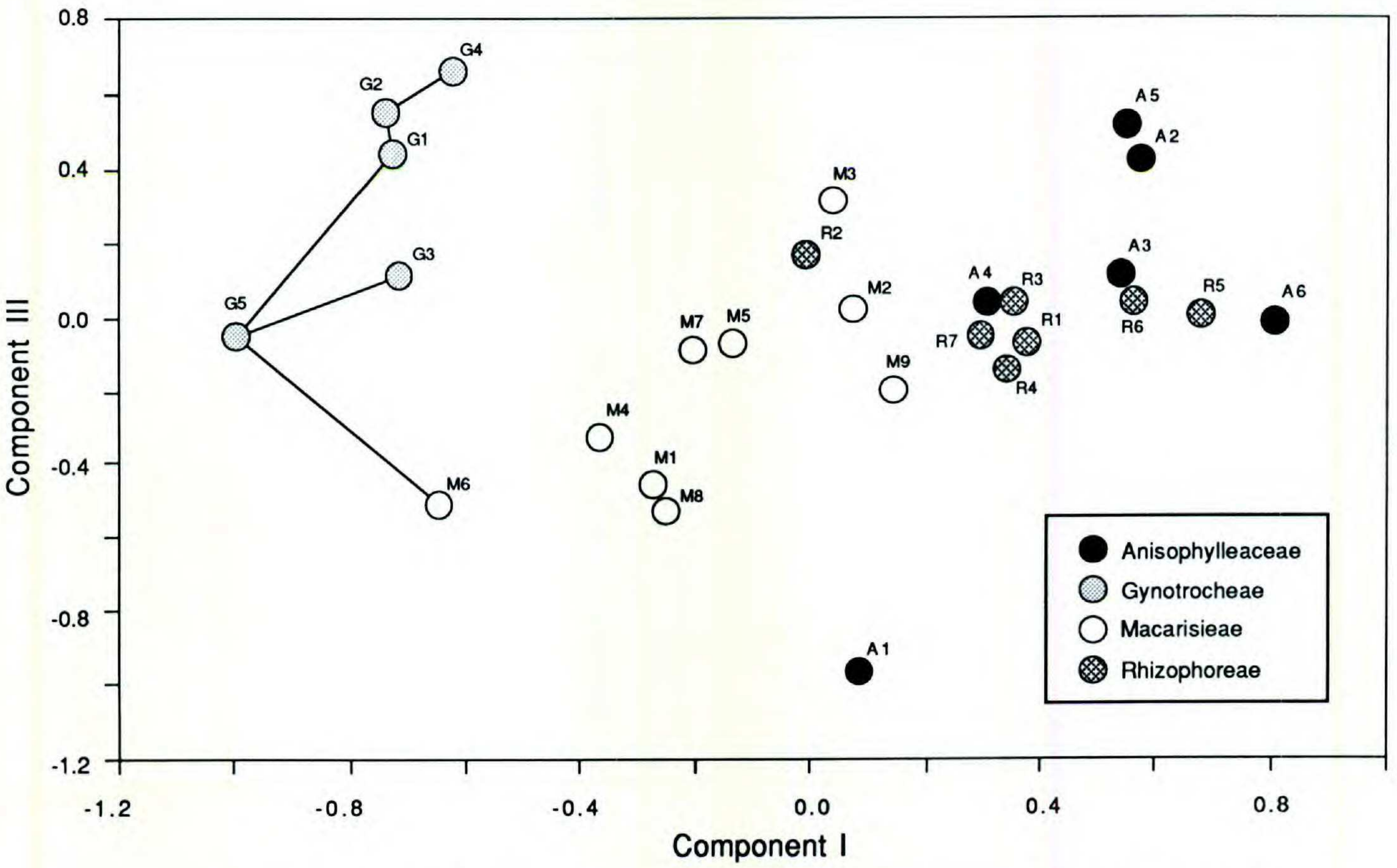


FIGURE 71. *Projection of same 27 OTUs (Fig. 70) onto principal components I and III. Percent of variation expressed by component III is 13.0. A partial minimum spanning tree has been included to clarify relationships within Gynotrocheae.*

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